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THE TREND OF HUMAN EVOLUTION

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ACCELERATION AND DECELERATION IN THE RATES OF EVOLUTION

In his book, "Tempo and Mode of Evolution," G. G. Simpson states (p. 125) that while most phyletic lines evolve regularly at rates more or less comparable to those of their allies, some lines seem to evolve with exceptional rapidity while others change so slowly that they hardly seem to be evolving at all. The simultaneous occurrence in the recent fauna of generalized lemuroids, specialized and aberrant lemuroids, and many monkeys, few apes, and the unique species of man can be explained, according to the author, only by the postulate that the more primitive lemurs evolved more slowly, and apes and man more rapidly, than the average rate for primates.

There are very good examples for such differences in the rates of development of monkeys, apes and man despite the scarce fossil material available in the higher primate groups. In Locality I of Choukoutien, for example, several skulls of macaques have been recovered which differ only in size and robustness from macaques living today in North and West China (*Pithecus tibetanus* and *Pithecus lasiotis*). This fossil macaque, described by C. C. Young as *Macacus robustus,* because robustness is its only characteristic feature, was contemporaneous with *Sinanthropus pekinensis* and shared its habitat with him. Nevertheless, except for a relatively slight reduction in size and robustness, the macaque does not present any change in the basic character of its essential features over a period of about 500,000 years, while Sinanthropus, as an early hominid type, underwent great changes during the same period. So we have an almost complete standstill in one case and rapid development in the other. It seems very likely that orangutan and Pithecanthropus contrast in the same way. Except for the size of the teeth, the fossil orangutan from South China and Java scarcely differs from the living orangutan while Pithecanthropus changed in almost every detail during the same period, retaining only his general human character.

Another example which could be interpreted as a standstill in evolution is the case of *Paidopithex rhenanus. Paidopithex rhenanus,* represented by a well preserved femur, is a fossil primate from the Lower Pliocene of the valley of the Rhine. Its general form, proportions, and every detail are identical with those of the femur of recent *Hylobates* (gibbons) of South Asia and Indonesia, the only differences being the size of the *Paidopithex* femur which is much larger

than that of any living *Hylobates*. This fact proves that a typical gibbon, already specialized, had evolved in the Tertiary without, in the meantime, changing its essential morphological character.

Even modern man himself would seem to have stopped his evolution at the beginning of the Pleistocene if the fragmentary braincases of Piltdown (England) and Kanam (East Africa), which show all the morphological characteristics of modern human skulls, really belong to the geological horizons from which they have been taken. This would mean that the modern type of man discontinued evolution for a period of at least five hundred thousand or even a million years. If a change of environment could be responsible for discontinuation or reassumption of evolutionary courses, as many people claim, then it must be presumed that the environmental conditions in England and East Africa, so far as man is concerned, were the same during the whole Pleistocene period, which is certainly not true. In addition, such a spatially limited standstill in human evolution is even less probable since incontestable facts prove that human evolution did proceed relatively rapidly at the same time in other regions (China and Java) although the environments cannot have differed essentially from those in East Africa.

People who believe in such an early appearance of the modern type of man always use the same means to invalidate facts contrary to their theory. Since the first human fossil came to light there have been claims that forms which were more primitive but geologically more recent than more advanced forms living earlier, have stopped evolution forever. For this reason they have to be assigned to another human "species" or "genus" than the unknown one which led to modern man. Such fossils are interpreted as remainders of long extinguished forms, natural experiments that failed.

If this were true, no essay on the trend of human evolution could be written. However, as more fossil material comes to light it becomes more and more evident that each morphological feature characteristic of modern man can be traced back to fossil forms to which recognition as human ancestors had been denied by somebody. This tracing leads to earlier stages whose specificities get more and more lost by merging into a "generalized" simian pattern. In addition, none of these features is independent. All are closely correlated, irrespective of the evolutionary stage in which they are observed. The maintenance of their correlation proves that any change of any individual feature must depend on changes in other features. It is just this persistence that makes the tracing possible. Were specific features nothing but accumulations of structural peculiarities varying at random in each stage without keeping to their original correlations, no evolutionary trend would be recognizable.

Specialization and Correlation

Human evolution is specialization. If modes of evolution exist in which no specialization takes place, man does not belong to such a category. Therefore the trend of man's evolution is determinable if the type of his specialization is known and can be traced back to its first manifestation. The organization of the human body, and the static and dynamic conditions to which the whole body and its individual parts are subjected, are better known than those of any other creature. This knowledge permits recognition of the function of every structure and the effect that eventual changes in one structure may have on all the others to which this structure is correlated. Any organization whatsoever can work only if all parts of which it is composed are adapted to each other and cooperate harmoniously.

The fundamental specialization by which man differs from any other mammal, and particularly from those which come closest to his own organization, is the perfectly erect position and the complete release of the forelimbs from use

in the locomotion of the body. "Bipeds" occur in fossil and living reptiles, birds and mammals. In the first two classes, however, upright posture is confined to the prepelvian part of the skeleton, while in all cases the pelvis itself and the hind limbs retain their original quadruped orientation and corresponding structural peculiarities. In some primates, upright stance and gait, with or without auxiliary support of the forelimbs, have been achieved. But in man alone the heels rest on the ground; the legs are stretched in hip and knee joints to the maximum extent; the pelvis is tilted forward; the vertebral column is curved alternately forward and backward; and finally the skull rests with the center of the base on top of the spine (figure 1c).

A perpendicular dropped from the vertex of the head when the body is in a relaxed posture runs through approximately the atlanto-occipital joint, passes tangentially the cervical and lumbar convexities of the spine and goes nearly through the hip joints and the knee and ankle joints. In a forced extension of the whole body it runs through the spine and all the joints mentioned. In addition, the legs are adduced to the midline so that knees and ankles touch each other. In such a posture the center of gravity is placed within the perpendicular near the promontory of the pelvis, and the weight of the body is carried in equilibrium by the pelvis and the legs. By this arrangement the least possible muscular energy is required to keep the body in balance, and the tension of fasciae and ligaments is used to substitute for muscle action. In the semi-erect position of dinosaurs, birds and kangaroos a similar principle has been applied by ossification of the tendons of the dorsal muscles of the trunk and of the leg. None of the anthropoids, apes or monkeys is capable of

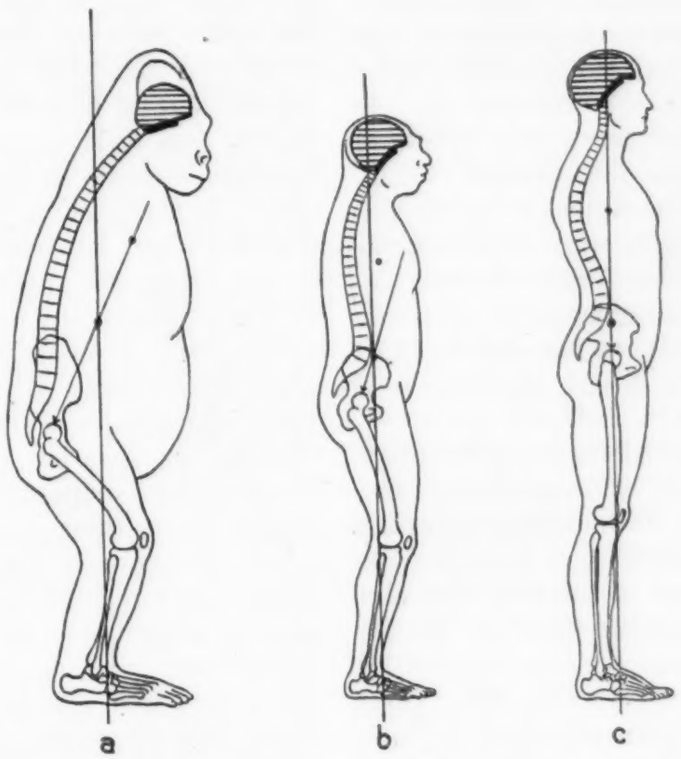

FIG. 1. Gorilla (a), Neanderthal Man—La Chapelle-aux-Saints (b), modern man (c) in erect position. After J. Dudley Morton (the human foot, 1935).

The axes and the location of the center of gravity are indicated. Situation of cranial cavity and base of braincase roughly indicated after F. Weidenreich.

taking the same posture as man. The construction of the individual bones of their skeletons, their proportions and their arrangement, have not entirely lost the original quadrupedal character (fig. 1a).

Practically all individual bones of the human skeleton give evidence of their adaptation to the special statics and dynamics of upright posture. Even minute details may owe their shaping to these factors. Foot bones as well as cranial bones are built in accordance with the particular requirements of their location and function. In the vertebral column, not only the form of the body of the vertebrae but also the direction of their articular facets and that of their neural spines, depend entirely on the place the respective vertebrae occupy in the carrying system of the trunk. For thirty-five years I have studied the human skeleton in order to find out how far form and features of the individual bones answer to the special requirements of the erect position. I studied the pelvis (1913), the foot and the lower extremities (1921/1922), hand and foot (1931), the spine and the skull (1924), and the general effect of muscular action on the skeleton (1922). The result of these studies is the conclusion that the shaping of each of even the simplest units of the human skeleton depends upon that of other units, that is to say, that all are strictly correlated and fit perfectly with the special organization of the body.

Most of my contributions to the problem of correlation and adaptation have been ignored, even by authors dealing with the same question, perhaps because they were written in German, but certainly also because the time had not yet come for an approach to the problem of evolution from the functional side. Considerations that were suspected as "Lamarckian" were banned. Nevertheless, only the functional approach to morphological problems will lead to the understanding of specific forms such as those of man, and their changes in the course of evolution. All those interested in studies of this kind are referred to a paper recently published by the Dutch author, E. J. Slijper. In this investigation, the author deals with the vertebral column and the spinal musculature of mammals, and shows conclusively that their specific form depends entirely on the special static and dynamic requirements of locomotion.

Since completely erect posture represents the specialization typical of modern man, and all skeletal bones are correlated and adapted to that position, any basic deviation from the stance and gait of the type must become manifest by differences in the construction and form of the individual bones. In other words, if man has derived from a primate whose physical organization was genuinely that of a quadruped, man's forerunners, wherever and whenever they may have lived, must display quadrupedal characteristics of the skeleton. The more remote they are from the most recent—most adapted—form, the more they will show them, or the other way round: the quadrupedal characteristics must be more obscure and the bipedal ones more obvious the closer the forerunners come to the modern human type. If the gradual changes of these characters can be determined, one way or the other, the trend of phylogenetic evolution of man will be evident by mere comparison. Nothing is known so far about those earliest phases in which features, recognizable without any doubt as "human" in character, are dawning. All that has been written about, and all the names given those hypothetical archetypes, are nothing but phantoms construed from deductions from the anatomy of present man and his immediate predecessors. Living and fossil human forms must have retained some structures of the most "primitive" primates, but the correct phylogenetic interpretation of these traces depends on the recognition of the character of their functional changes.

1. *Extremities and trunk*

The foot is that part of the human skeleton whose structural details should give the most reliable information of its original appearance before it was adapted to an erect position. The arrangement of the tarsal and metatarsal bones and their forms are still those of a five pronged instrument constructed for grasping and keeping objects in its grip, like a hand. This is the functional meaning of the longitudinal and transversal arches of the foot and the decrease in length of the metatarsal and phalangeal rays. The human foot still possesses all the muscles necessary to spread and flex the toes and abduct or adduct the hallux despite the loss of their ability to act in this way. In addition, although all the original foot joints are still functioning, their mobility has been greatly restricted or arrested. At the same time, the muscles have been replaced in part by ligaments and fasciae wherever the static and dynamic conditions allow for such a substitution. In this way, a restricted mobility but a greater stability, and, above all, elasticity, have been achieved. These are exactly the prerequisites for securing the support of the body on such a small base as the human foot offers in bipedal stance and gait.

As the center of gravity shifts backward (cf. fig. 1a and c), a result of the adoption of the erect posture, the heel bone is pressed down to the ground and strengthened in its new task by a substantial increase in height and a broadening of its base, the *tuber calcanei,* to enable it to carry the body weight. Thus the tuber, and only the human tuber, has developed an accessory process on its lateral side—*processus lateralis tuberis calcanei.* In none of the anthropoids, not even in the mighty gorilla, does such a process exist, the tuber being represented here only by a medial process (Weidenreich, 1921/22, 1940). The relatively late acquisition of the lateral process follows from the fact that not even in living man are the two structures merged into one but may remain more or less separated. Unfortunately, the position of the lateral process and its relation to the medial one cannot be checked in fossil man. Only two or three heel bones have been recovered with the region in question preserved. They belong, however, to late Neanderthal phases or to fossil neoanthropic man,[1] and for this reason do not differ essentially from those of modern Australians in which the lateral process is occasionally completely isolated.

The precise evolutionary phase in which man lost the grasping (climbing) character of his foot is a matter of speculation. Probably it happened at a very early period. Such an early dating can also be inferred from the state of other bones of the lower extremities. Although the material on hand is very scanty, and foot and hip bones are missing in all Archanthropines,[1] the character of the two tibiae of *Homo soloensis* and of several fragmentary femora of Sinanthropus prove that these types had passed the climbing and quadrupedal stage of locomotion long ago. They all exhibit structures characteristic of a creature walking erect. Neither in their proportions nor in any other peculiarity of their extremities have they retained any clear simian feature. It is true the limb bones differ from the standard type of modern man in some minor details, but the deviations are not of a kind to exclude erect position. Therefore, Eugène Dubois, who gave Pithecanthropus the surname *"erectus,"* may have been right although it still remains doubtful whether the Trinil femur is typical of Pithecanthropus and may not be the femur of a more advanced human form which was accidentally de-

[1] The term "neoanthropic" man is used for the modern human form. "Paleoanthropic" man means the immediately preceding group of fossil man, the Neanderthalians and corresponding groups. The term "archanthropic" man comprehends all the forms of early hominids who precede the Paleoanthropines (cf. Weidenreich, 1946).

posited at the same site as the skull fragment.

The only hip bones and vertebrae known are those of Paleoanthropines.[2] The former show the usual neoanthropic pattern indicating that the pelvis must have been subjected to the static and dynamic conditions of erect position for a long period of time. Regarding the vertebral column, the best known is that of the man of La Chapelle-aux-Saints, described and reconstructed by M. Boule. As the special features of the individual vertebrae which indicate the degree of the cervical and lumbar curvatures of the column (see above) show no essential deviations, Boule modeled the column after the general modern pattern. But, since he found some of these features of the individual vertebrae less pronounced than they are in the majority of human individuals of today, he bent the model column slightly forward (fig. 1b). I do not believe that Boule's reconstruction is representative of all Neanderthalians. Indeed, McCown and Keith state with regard to the lumbar curvature of the Mount Carmel population: "Our evidence points to this curvature being developed at least to the extent found in modern native races." Boule, however, may be right so far as the posture of the skull is concerned. Size, length and direction of the neural spines of the cervical vertebrae suggest that the muscles attached to them may have been considerably stronger than those of neoanthropic man. The formation of the nuchal region of the archanthropine skull lends strong support to such a suggestion. Early man was certainly bull-necked.

The character of the bones of the upper extremity of Archanthropines and Paleoanthropines fits in well with that of the lower extremity. Humerus, clavicle and one wrist bone of Sinanthropus, the only upper extremity bones of Archanthropines preserved, completely conform to those of neoanthropic man in form and proportions, and the same is true of the upper extremity bones of the Neanderthalians. It may be that these bones are a little longer in proportion to the leg bones but they certainly do not fall outside of the limits of normal variation found in modern man.

To summarize what we know of the skeleton of trunk and extremities of fossil man, all specimens display a neoanthropic pattern; therefore it can be taken for granted that man achieved upright position as soon as he became morphologically discernible as man. The long bones of the lower extremity are much more robust in the earlier stages than in any of the neoanthropic forms. The femur of Sinanthropus, although not exceeding that of the neoanthropic type in circumference, excels in the thickness of its compacta and a corresponding narrowness of the medullary canal. These properties are indications of a greater massiveness of the skeleton of early man. We will return to this question later.

2. *The skull*

The only skeletal part of early man that does not show the same degree of adapta-

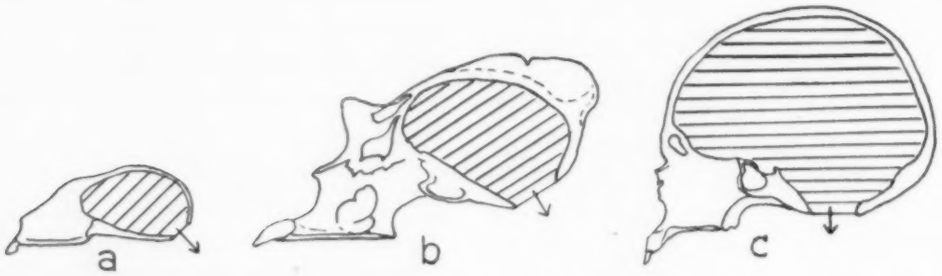

FIG. 2. Mid-sagittal sections through the skulls of lemur (a), gorilla (b), and modern man (c), showing the differences in the topographical orientation of braincase and face. In part after W. L. H. Duckworth.

tion to upright position as do trunk and extremity bones is the skull. Among the primates the skull of the lemurs comes closest to the original quadrupedal mammalian type (figs. 2 and 3a). The two main constituents of the skull, the braincase and the face, are arranged in a straight horizontal line so that the snout (upper and lower jaws) is in front and the braincase continues into the spine in the rear. The change in the manner of locomotion and the adaptation of the skull to the erect position require a fundamental alteration in the primary topographical arrangement of the two constituents of the skull. If the spine passes from a horizontal orientation to a vertical one, and the skull joins in this movement without abandoning its original connection with the spine, the face would be placed on top of the skull and the eyes would look upward. Of course such a twisted posture could be corrected by bowing the head to such an extent that the longitudinal axis of the skull would form a right angle with the longitudinal axis of the spine. Such a position, however, would consume the total range of mobility of the atlanto-occipital joint. Nature used another way of adaptation. The base of the skull itself has been deflected to maintain the connection between the occipital part of the braincase and the spine. The rest has been brought into a horizontal line and the face reduced in size and length to such an extent that it could be lodged almost entirely beneath the deflected front part of the braincase (figs. 2 and 3c; 5).

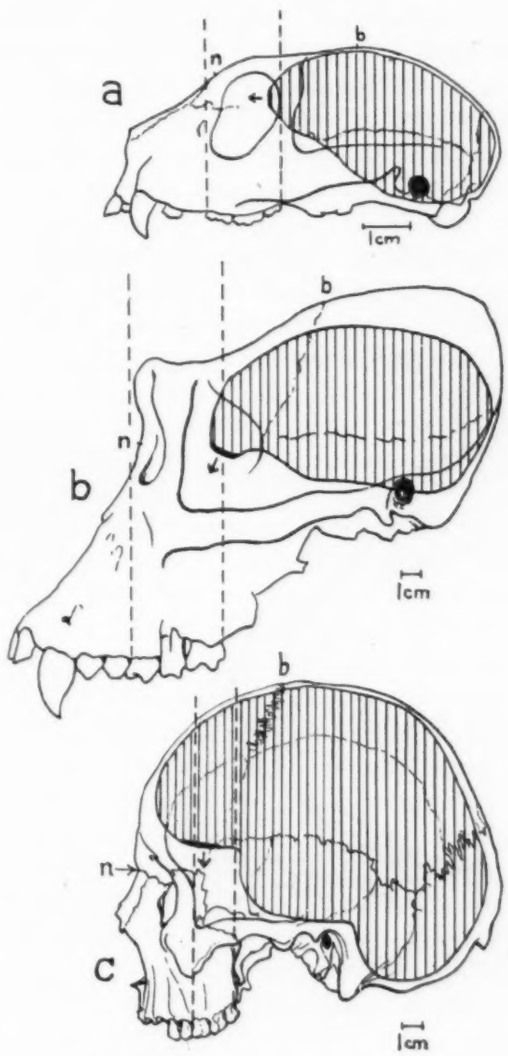

FIG. 3. Skull of lemur (a), gorilla (b), and modern man (c), in lateral view, showing the differences in the topographical orientation of braincase and face and in the orientation, size and form of the brain (cranial cavity shaded). The different directions of the olfactory nerves (lamina cribrosa) are indicated by arrows. b—bregma, n—nasion.

The original quadrupedal character of the skull must have been lost long before the human stage was reached. In monkeys and apes the frontal pole of the braincase has already been raised and overlaps the rear parts of the facial skeleton (figs. 2 and 3b). This slanted position of the braincase corresponds to the semi-erect posture of the trunk. All the known skulls of the Archanthropines have already passed this simian stage. Only the foremost parts of the eyesockets are still thrust beyond the frontal pole of the braincase. The vigorously strengthened upper margins of the "exposed" eye sockets—*tori supraorbitales*—one of the most conspicuous features of this phylogenetic stage of human evolution (fig. 4b), and a slight "facial prognathism," are all that has been left from the protruding snout of the simian stage.

The base has not reached its maximum deflection in either the Archanthropines nor in the classic Neanderthalians. The deflection is only completed in neoan-

thropic man. The form of the original human braincase, such as is typical of the Archanthropines, is comparable to a flat, oblong, loaf-like body. Its neoanthropic form is more globular. The transformation looks like a "rolling-up," that is to say, the flat, loaf-like braincase bends around a transverse axis which runs approximately through the mandibular joints of both sides. In this way the frontal and occipital poles move closer together, resulting in the reduction of the length of the base and the lifting high up of the apex of the curvature (fig. 5). All individual cranial bones undergo corresponding changes in their proportions, forms and topographical relations. The base of the temporal bone, situated in the center of this "movement," is the most affected in all its details. As long as the braincase is stretched and flat, the temporal base occupies a greater area between the sphenoid and occipital bones. When the skull is rolled up, the whole basilar part of the temporal bone is jammed between the adjoining bones and at the same time is pushed up into the cranial cavity. The characteristic changes which the individual portions of the temporal bones undergo as a result of this process have been described in an earlier paper (1943). Their state can serve as a standard for the degree of transformation at-

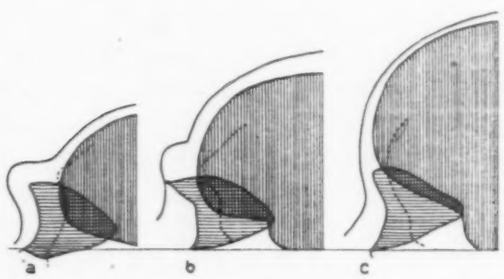

FIG. 4. The topographical relation between orbit and cranial cavity in chimpanzee (a), Sinanthropus (b), and modern man (c). The brain (vertically lines) expands forward and overlaps the orbit (horizontal lines). The supraorbitals disappear correspondingly.

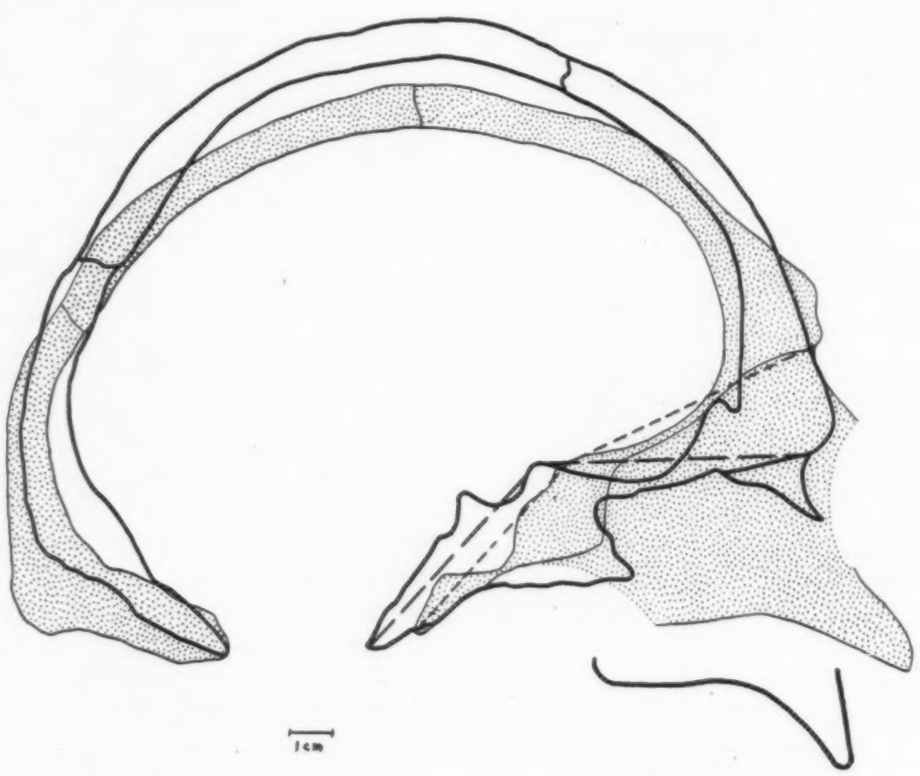

FIG. 5. Mid-sagittal diagrams of the skulls of *Homo soloensis* Skull XI (stippled) and modern man—Tasmanian (heavy lines), showing the differences in the deflection of the base (indicated by interrupted lines), the shortening of the base and the vertex elevation of modern man. The face of Sinanthropus has been substituted for the missing face of *Homo soloensis*.

tained by the skull and, consequently, as a clue for the classification of the type.

Concomitant with the transformation of the braincase, the face recedes beneath it (figs. 2, 3c and 5). The mighty supraorbitals disintegrate correspondingly (fig. 4c) until nothing is left but a faint swelling at the medial part of the eyebrow region—the superciliary ridge. The facial "prognathism" becomes further reduced to "orthognathism" and "hyperorthognathism," and the cheeks appear correspondingly more "sunken." The nasal bridge, the anterior nasal spine, and the chin, jut out from the profile as the remaining foremost landmarks of the otherwise shrunken face.

3. *Dentition*

Almost all the alterations of the dentition in the course of the phylogenetic evolution of man can be regarded as a consequence of the reduction of the face and of its adaptation to the upright position. The dentition of the earliest hominids differs from that of the anthropoids, living or fossil—with the exception of the Australopithecinae—by having no tusk-like canines and no sectorial-typed first lower premolars. But they agree with them in the general pattern of the lower molars. They agree, furthermore, with the gorilla, but not with the orangutan and chimpanzee, in having small incisors but large molars. Crown and roots of the Archanthropine teeth, especially those of the giant forms, far exceed in size those of neoanthropic man. Reduction is already apparent in the Paleoanthropines. The shortening of the jaws necessitates a shortening of the entire row of molars and a shortening of individual teeth; the last of the row, the third molar, being particularly affected, becoming smaller in all dimensions. In the paleoanthropine Heidelberg jaw this molar is already reduced to an extent characteristic of modern man. In the other teeth the shortening of the length results in a relative increase in height. The reduction of the crown pattern appears as a progressive simplification with the number of the molar cusps decreasing and the originally complicated wrinkle system becoming ironed out. In modern man the third molar tends to disappear entirely. In many cases its eruption is delayed or never occurs, or the tooth does not develop at all. Exactly the same process takes place in the dog. Dwarf dogs, compared with large dogs, have undergone a remarkable reduction of the molars in number, size and details of their pattern (simplification); the reduction of the teeth here goes hand in hand with the reduction of the jaw and the transformation of the braincase in the wake of the relative enlargement of the brain (Weidenreich, 1941).

4. *Robustness of the bones*

Two of the most typical features of the cranial bones of early man is their thickness and massiveness (Weidenreich, 1942, 1947). These qualities are not confined to the bones which build the walls of the cranial cavity but include the whole facial skeleton. The thickness and massiveness is chiefly due to the thickening of the outer and inner tables of the cranial bones, while the mass of spongy substance between (diploë) is small in comparison with the condition in modern man. In the lower jaw of Meganthropus the density of the enormously thickened compacta layers looks almost like an eburnation. The mass of the supraorbitals, however, consists mainly of dense spongious substance. The cranial bones of the Archanthropines exceed by far those of all known Paleoanthropines in thickness and massiveness. Meganthropus, *Pithecanthropus robustus* and *Homo soloensis* top the list for robustness, *Pithecanthropus erectus* and Sinanthropus follow. The extraordinary robustness of all these different early types—evidently still surpassed by the cranial bones of Gigantopithecus of which only some of the teeth are known—suggests that this robustness is not an accidental variation but represents a general character of earliest homi-

nids. The shafts of the femur of Sinanthropus and the tibia of *Homo soloensis* indicate that it was not confined to the bones of the skull but may also have affected the extremities. This type of robustness does not show in living anthropoids nor in any other living primate but there is some indication that it may have occurred in certain fossil primate forms (Australopithecinae, Dryopithecus). Although it is not yet possible to tell from whom the hominids inherited this special feature, what happened to it in the course of subsequent phylogenetic evolution can be described. A tendency toward reduction has already set in within the Archanthropine group itself, as *Pithecanthropus erectus* and Sinanthropus reveal. The clumsiness of the Rhodesian skull, the Heidelberg jaw, the general thickness of the Neanderthalian skulls and the robustness of their femora demonstrate that the old Archanthropine feature in question is still recognizable although it has lost much of its original character. The reduction continues even in neoanthropic man: it is less in upper Paleolithic man than in recent man, less in "primitive" races than in more "advanced" ones of present mankind. In the temporal bone the reduction generally reaches a high degree: the apex region of the pyramid appears eroded and a wide "*foramen lacerum*" takes its place; the tympanic bone, which is a thick plate in Archanthropines, is almost paper thin and not infrequently even perforated (Huschke's foramen). But the original thickness of the bone seems to be preserved in some special places. I interpret the so-called ear exostoses at the entrance of the *meatus acusticus externus* as such relics. The *tori mandibularis* and *palatinus* may be interpreted in the same way.

Another phenomenon, very characteristic of the Archanthropines, which may have some connection with the robustness of the cranial bones, is the early closure of the sutures. In all the Archanthropines the main sutures are ossified and in most specimens fused to such an extent that they are scarcely recognizable from either inside or outside. Under similar conditions in modern man, the cranial sutures are either open or just at the beginning of fusion. Complete ossification of the cranial sutures, even their entire disappearance at an early stage, is typical of anthropoids.

5. *The brain*

It follows from all the recorded facts that the adoption of upright position and the correlated adaptation of all skeletal parts is the fundamental specialization of man. There is, however, a second one seemingly partially correlated to the first but surpassing it in significance. This is the enlargement and differentiation of the brain. However, the trend toward the expansion of the brain, particularly the pallium, in the course of evolution is not a privilege of man or the primates. It is a characteristic feature of many mammals and also apparent in reptiles and birds. As early as 1876, O. C. Marsh made the following statements: (1) All mammals at the beginning of the Tertiary had small brains; (2) the size of the brain gradually increased during the Tertiary period; (3) this increase was confined mainly to the cerebral hemispheres . . . ; (4) in some groups the convolutions of the brain have gradually become more complex; (5) there is some evidence that the same general law of brain growth holds good for birds and reptiles from the Cretaceous to the present time. The paleontological facts which have come to light in the meantime have largely corroborated the truth of Marsh's theses. However, the mere increase in size is not that specialization of the human brain upon which all physical development and achievement depend. All attempts to read the degree of mental efficiency from morphologically recognizable features such as size or form of the brain or of its lobes or of the convolutions, have failed. It can only be said that a certain amount of brain substance is necessary for normal psychical functioning.

Anthropoids with a maximum cranium capacity of 650 cc. behave like apes and a living adult human being with no more brain may operate its vegetative system but is an idiot. Pithecanthropus, the most primitive human form whose brain size can be calculated, has a cranial capacity of 775 cc. (Skull II). Provided that mental faculties are only a matter of the amount of brain mass, the doorstep to humanity would be passed if the cranial capacity lies between 650 cc. and 750 cc. On the other hand, the maximum brain size attained by a fossil non-neoanthropic hominid is 1620 cc. (Man of La Chapelle-aux-Saints). However, this increase of about 900 cc., tantamount to the size of the Pithecanthropus brain, cannot be taken as a measure of man's cerebral specialization or progress in phylogenetic development. For among adult neoanthropic men with normally functioning brains, the cranial capacity ranges from about 900 cc. to 2000 cc. Nobody has ever been able to tell which internal structures of the brain allow a margin of half of the possible total amount for normal or even supernormal functions. The list of "elite" brains includes famous personalities whose brain mass or cranial capacity ranges from 1100 cc. to over 2000 cc. There is a certain relation between brain size and body size; tall individuals may have larger brains than small individuals, yet small individuals may also have relatively large brains. However, these differences are minimal when compared with the normal fluctuations of brain size and can, therefore, be disregarded. In addition to all this, there are no data which prove incontestably that the human brain gained in average size between the paleoanthropic and neoanthropic phases. The most reliable figures available indicate instead a slight decrease.

All these discrepancies are easier to understand if it is realized that operation and regulation of the vegetative system of the human body require a very small amount of brain substance, as the brains of idiots indicate. Adult idiots may do it with not more than 350 cc. The brain substance exceeding this amount seems, therefore, available for psychical functions. These functions have their main seat in the cells of the cerebral cortex and in the fiber systems. To my knowledge, however, no investigation has ever been made to find out whether there is a constant relation between the total size of the brain or that of the pallium, and the efficiency of the cortex and fiber systems, and if not, how the brain can fulfill all its mental potentialities whether it weighs 1100 gr. or 2000 gr.

In any case, the latest phase of specialization of the human brain must take place in the cortex and be independent of the actual size of the brain and, consequently, also of that of the braincase. The main morphologically recognizable difference between the brain of Archanthropines and the brain of Paleoanthropines is the greater fullness of the latter (Weidenreich, 1947). All parts of the pallium have a share in the enlargement, the four lobes in almost equal proportions. But there is no change in the general form. All the brains of the evolutionary stages preceding the stage of modern man are flat and show no vertex elevation irrespective of their absolute length or their vertical diameter, the latter rising from 95 mm. in Pithecanthropus II to 116 mm. in La Chapelle-aux-Saints.

A characteristic change of the brain occurs, however, before the definite stage of neoanthropic man has been reached. Its vertex rises to a hump-like elevation while its total length shortens. This is the result of the "rolling up" of the braincase, the deflection of the base, and the final adaptation to upright position as has been described above (cf. fig. 5). But there seems to be no direct correlation between the increase of the cortex differentiations and the special shaping of the brain. Neither is the growing fissuration of the pallium correlated to it. This phenomenon is a part of the general expansion of the brain in the course of evolution and accordingly takes place in most mam-

malian orders. The folding process of the cerebral surface first produces the main divisions, the lobes, and then the subdivisions, the convolutions. In primates the increase of the fissuration keeps pace with the advancing general organization of the subgroups and so complements the expansion of the pallium in cases in which the space for the expansion of the braincase itself is limited. Among the primates, man has the most expanded brain, the most developed and complicated fissuration and, in accordance therewith, the most highly differentiated cortex structures.

But man exceeds all vertebrates including the primates in another feature which so far has escaped attention. Man has the smallest spinal cord in proportion to the size of the brain. In the course of evolution the human brain has "swallowed" the spinal cord, that is, it took over the functions of the latter more and more, bringing the reflex actions under the control of consciousness and will. Unfortunately, the gradual diminution of the cord cannot be tested in fossil man for the vertebral column is missing or does not permit calculations of the volume of the vertebral canal. But in living anthropoids the cord is clearly greater in proportion to the size of the brain than in man.

The transformation of the skull

The transformation of the human skull in the course of evolution follows a very definite line to which all essential structures hold, even in minute details. Not a single fossil human type has come to light which shows any indication of deviation from this line. Irrespective of the site from which the specimens were recovered or to what geological period they may be attributed, all exhibit the characteristics of the respective features either of the earliest stages or those of later or latest ones, the latter with the typical signs of disintegration of the original pattern. Dozens of examples can be given, but for want of space only one of the most conspicuous features, the *supraorbital tori* have been selected. As I have shown earlier (1939, 1943) these structures are the front part of a reinforcement system which originally runs around the braincase at its greatest circumference, the *occipital torus* representing its rear portion. In modern man the *supraorbital tori* have almost entirely disintegrated, a small swelling at the medial ends of the eyebrows is all that is left. What the tori looked like at the very dawn of mankind is unknown, but we may not be too far afield in suggesting that their formation was similar to those of the living gorilla (fig. 6a): a strong, exceedingly protruding and continuous bar crossing the forehead at its base along the margins of the orbits. Their lateral ends jut far out while behind them the braincase shows the characteristic postorbital constriction. Viewed from above, the bar exhibits a distinct forward directed convexity. In the Archanthropines (figs. 6b, c, d) the front contour differs from that of the gorilla (a) by forming an almost straight line and having the lateral ends considerably thickened. But *Homo soloensis* (d) already indicates the beginning of the disintegration of the torus by breaking its continuity into two separate portions, a process which is in full swing in the Paleoanthropines (e, f). At the same time, the tori shrink and their ends bend backward to conform more and more to the rounded front contours of the braincase proper (see also fig. 4c). The postorbital constriction disappears to the same degree. The disintegration is completed in the final stage of neoanthropic man.

Nothing can better prove the unity of the hominid type than the study of gradual changes of features such as this one. People who deny the unity and imagine that *Homo sapiens* did not derive from a Neanderthalian or Sinanthropus type and that, therefore, features like his superciliary ridge are not necessarily relics of the supraorbital tori of earlier hominids but may be a newly developed ornament, are not sufficiently acquainted with comparative anatomy. Figure 6 also gives two ex-

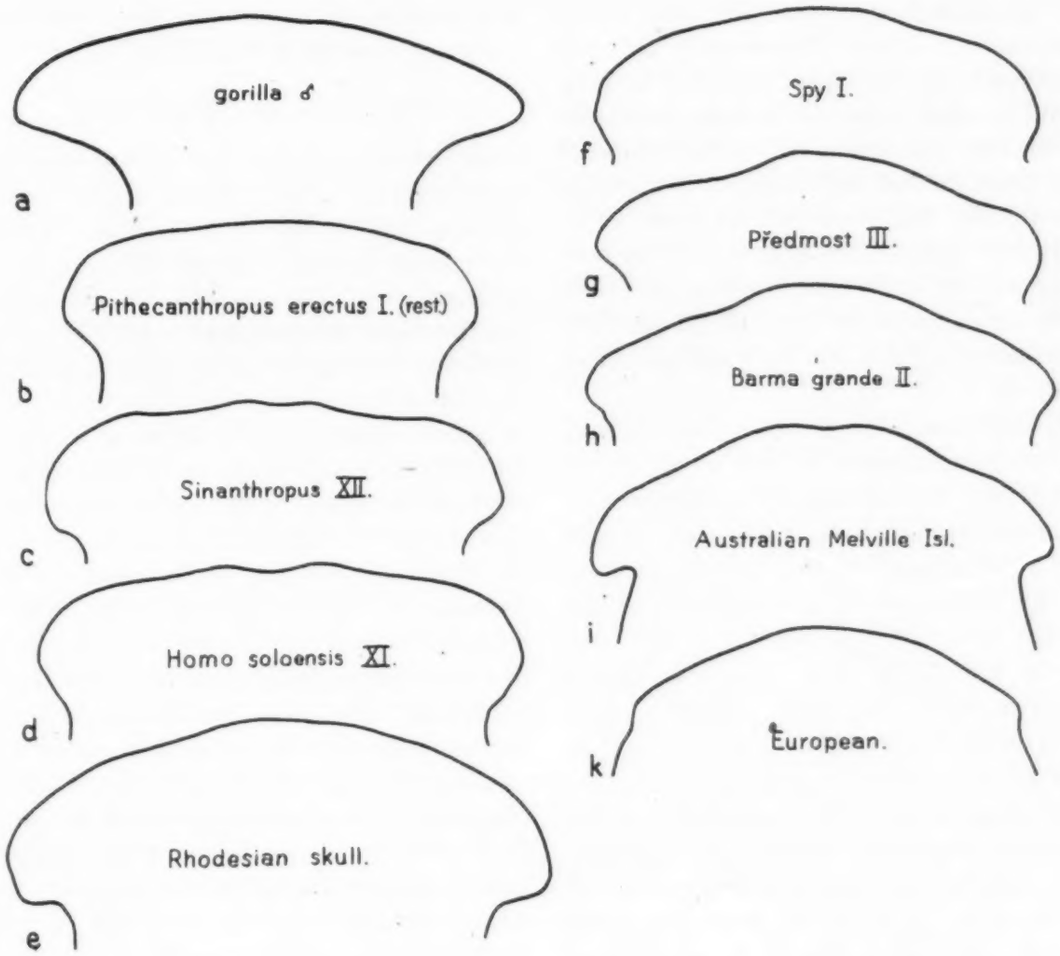

FIG. 6. The gradual disintegration and disappearance of the supraorbital tori in the course of human evolution. The tori viewed from above.

amples of Upper Paleolithic *Homo sapiens,* the Předmost Skull II (g) and the Barma grande Skull II (h). As all the features of these forms show, they are morphologically intermediate between the Paleoanthropines and living man. Despite all protests, negations or incredulity, none of the sceptics has been able to produce conclusive anatomical or biological evidence of specialization in any fossil hominid which would not fit the scheme of human specialization described and would lead definitely away from the established line of human evolution.

Figure 6 illustrates, in addition, another phenomenon characteristic of human evolution. The skulls depicted, Rhodesian (e) and Australian aborigine of today (i), show an extraordinary development of the supraorbital tori in the first case, and its equivalent, the superciliary ridges, in the second case. They contrast strikingly with other representatives of the phylogenetic groups to which they must be attributed on account of the character of other features they exhibit. The supraorbitals of the Rhodesian surpass in heaviness even those of some of the Archanthropines, nevertheless the curvature of the front contour conforms to that of the Paleoanthropines to which the skull belongs morphologically. In the Australian skull, the "superciliary" ridges are even more pronounced than in neoanthropic Upper Paleolithic man (cf. i with g and h), not to speak of modern Europeans (k). Reversions like these are common and well known occurrences. If they oc-

cur in neoanthropic man they are called "atavisms." Such "atavisms" are not confined to neoanthropic man but may be found in each phase of human evolution. When they are found in Archanthropines they point to still unknown earlier forms. Their mere existence proves that seemingly new features are not necessarily new creations but may have their roots in the past. It seems to me that not all students of human evolution are fully aware of this truth.

In addition to these reversions there is another phenomenon in human evolution which has not attracted the attention it deserves, particularly when the factors and mechanisms of the transmission of specific characters to descendants are discussed and interpreted. It has been shown that there is a strict correlation between almost all those features. It is superfluous to emphasize that such a correlation must exist in every evolutionary stage to guarantee the workability of the organism regardless whether it is already fully adapted to new conditions or still on its way. Considered from this point of view, it seems difficult to understand that some features which are typical of later stages of evolution can make their appearance in earlier stages although other features which are parts of the same correlated system still maintain their original character.

In the lower jaw of Sinanthropus the mental spine, a typical structure of modern man, is almost perfectly developed, although the chin, which is combined with the spine in modern man, is still missing. The strong *occipital torus,* one of the most characteristic features of the Archanthropines and an essential piece of the reinforcement system of the braincase, may already be disintegrated in Paleoanthropines to a degree found in modern man, although the front piece of the same system (the *supraorbital tori*) remains intact. The reverse condition, the disappearance of the supraorbitals but the maintenance of the *occipital torus* can happen too, but this condition has so far been observed only in neoanthropic man.

Orthogenetic Evolution

All the facts presented prove that the specialization of man in the course of his phylogenetic evolution is twofold. There is first the general "bipedal specialization" consisting of the adoption of the erect posture and the adaptation of the whole skeleton and body to it, and second, a particular brain specialization consisting of an enlargement of the brain as a whole, in addition to an expansion of the cerebral surface—increase of its fissuration—combined with a high degree of cortex differentiation. So far as the brain is involved, the bipedal specialization causes an adaptation of the form of the brain to the basilar deflection of the braincase. Although the two specializations are morphologically distinguishable, it is impossible to say which one set in first. Apparently they proceeded hand in hand, both reaching their climax in the modern human type. Yet, as indicated above, the brain specialization is a more general biological character, not necessarily confined to man, while the bipedal specialization is typical only of man.

Considered as a whole, human evolution has taken an orthogenetic course; it tends to proceed in one direction without any indication of deviation. Should there be an aversion to the term orthogenesis because it may imply predestination, I have no objection to calling it "rectolinear evolution." The mystery behind it remains the same for there is so far no indication that the recognizable stages of transformation which succeeded each other, or the individual features which characterize each of the stages, take their origin from "chance variations." The strict correlation which is evident even in the smallest morphological details renders, in my opinion, that interpretation unlikely. Although the most primitive hominid forms known so far come close to the stage in which they become scarcely

distinguishable from "apes," they are already specialized as hominids.

Environmental Influence

This raises the question of whether, and how far, environmental conditions can be made responsible for the course taken by human evolution. All the facts produced by human paleoanthropology are certainly incompatible with many earlier statements concerning the effects of environment, especially so far as they refer to climate. For example, the ape-like forerunners of man living an arboreal life in tropical forests are said to have given up this habit when high mountains (the Himalayan range) rose and changed the climate to the effect that the forests on the arid slopes disappeared. The apes on the dry mountain side were forced to descend to the ground, walked around here and became hominids while those living on the slopes with high precipitation continued their arboreal life and remained, therefore, apes until today. If this were true, the remains of early man should be found in the arid regions north of the Himalayan range and the apes south of it. In reality, the most primitive types of man have been recovered from regions which never changed their tropical or subtropical conditions (South China and Java), while the orangutan remained their companion all the time.

Furthermore, it has been claimed that the Last Glacial Period which came over Europe forced the Neanderthal man, living there in the mild Interglacial, to use all his wits to escape the inclemencies of the new climate, and this exceptional strain of his mind made his brain grow so that man became *"Homo sapiens."* This sounds like a joke but this kind of reasoning was very common for a long time. In reality, the only direct morphological evidence of transitional forms between Neanderthal man and *"Homo sapiens"* came from Palestine (Mt. Carmel population), but these intermediate types lived there long before the Last Glacial and may never have passed through a real Ice Age.

Beside climate, diet above all things has been used to account for producing morphological transformations on a great scale. Yet what human evolution reveals does not lend support to this theory. All the Archanthropines were probably omnivorous. Sinanthropus, at least, was a hunter, living on meat and fruits (hackberries) and using fire. His eating habits cannot have differed greatly from those of primitive tribes of our day. Nevertheless man's dentition has changed considerably since (see above). Besides, it is difficult to comprehend how the patterns of the molars of apes and man could have been affected by a special kind or change of food. Almost all apes, and certainly all anthropoids, are frugivorous and take practically the same kind of food. Nevertheless, the pattern of their teeth is so specific that it can be used to identify each type. In addition, this pattern remains intact only for a very short fraction of the life span; it is usually worn away soon after the eruption of the tooth. Moreover, it has never been made clear how food can alter the entire chewing system (jaw bones, muscles, teeth, etc.) which represents an integral part of the skull and, as such, is demonstrably dependent on the special formation of the skull (see above).

The search of morphologists for environmental factors directing evolution lost much ground when the geneticists claimed that experiments on living organisms proved incontestably that acquired characters are not inheritable. The transmission of new characters would only be possible if these characters were the effect of changes of the genes. However, the essential question, which factors start the "mutations," remained unanswered as before. In any case it is hard to understand how "chance" mutations, meaning purely "accidental" hereditary changes, can work in such an elaborate correlative system as the human organization. They could do it only if the muta-

tions fitted in with this system but not many "chances" would be left in such a case. The usual argument that time allows for any chance mutation and its eventual establishment, is scarcely applicable to the rapidly proceeding final stages of human evolution. For the period of time in which the hominids passed from the early Archantropine stage to that of neoanthropic man did not last "millions of years" but not more than about 500,000 years (about 15,000 generations) as estimated from reliable geological data.

Summary

The trend of human evolution is toward specialization. This specialization is twofold. It consists: (1) in the adoption of erect posture and a strictly correlated adaptation of the entire human organization to this position; and (2) in the expansion of the brain, especially of the surface of the pallium, and in an intensive differentiation of the internal cortex structures. Human evolution took an orthogenetic course. The facts available do not indicate that environmental conditions played a decisive role in this development.

Literature Cited

Boule, M. 1911/1912. L'homme de la Chapelle-aux-Saints. Annal. Paleont., **6**: 111–172 and **7**: 21–192.

Marsh, O. C. 1876. Recent discoveries of extinct animals. Amer. Jour. Sc. and Arts, **12**: 59–61.

McCown, Theodore C., and Sir Arthur Keith. 1939. The stone age of Mount Carmel. Vol. II. The fossil human remains from the Levalloiso-Mousterian. Oxford.

Simpson, George Gaylord. 1944. Tempo and mode in evolution. Columbia University Press.

Slijper, E. J. 1946. Comparative biologic-anatomical investigations on the vertebral column and spinal musculature of mammals. Kon. Ned. Akad. Wet. Verh., 2nd sec., **42**, 5: 1–128.

Weidenreich, Franz. 1913. Über das Hüftbein und das Becken der Primaten und ihre Umformung durch den aufrechten Gang. Anat. Anz., **44**: 497–513.

——. 1921/1922. Des Menschenfuss. Zeitschr. Morph. u. Anthropol., **22**: 51–282.

——. 1922. Über die Beziehungen zwischen Muskelapparat und Knochen und den Character des Knochengewebes. Verhandl. Anat. Ges. Erlangen, 28–53.

——. 1924. Die Sonderform des Menschenschädels als Anpassung an den aufrechten Gang. Zeitschr. Morphol. u. Anthropol., **24**: 157–189.

——. 1931. Der primäre Greifcharacter der menschlichen Hände und Füsse und seine Bedeutung für das Abstammungsproblem. Verhandl. Ges. Phys. Anthrop., 97–110.

——. 1939. The torus occipitalis and related structures and their transformation in the course of human evolution. Bull. Geol. Soc. China, **19**: 480–558.

——. 1940. The external tubercle of the human tuber calcanei. Am. J. Phys. Anthrop., **26**: 473–487.

——. 1941. The brain and its role in the phylogenetic transformation of the human skull. Trans. Am. Philos. Soc. (Philadelphia), N. S., **31**: 321–442.

——. 1942. The massiveness of the prehominid skull; a distinctive hominid character. Am. J. Phys. Anthr., **29**: 318.

——. 1943. The skull of *Sinanthropus pekinensis;* a comparative study on a primitive hominid skull. Palaeontol. Sin., N. S. 10, whole ser., **127**: 1–484.

——. 1946. Apes, giants and man. The University of Chicago Press.

——. 1947. Some particulars of skull and brain of early hominids and their bearing on the problem of the relationship between man and anthropoids. Am. J. Phys. Anthr. (in press).

MORPHOLOGICAL VARIATION IN NATURAL POPULATIONS OF *DROSOPHILA ROBUSTA* STURTEVANT

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INTRODUCTION

For many years, the large size of populations, ease of collection, and economy in handling have made insects a favored group for the study of geographical variation. In those cases in which it has been possible to study the morphology, physiology, genetics and cytology of the same organism, studies of geographical variation have been particularly fruitful for the clarification of evolutionary relationships at the species and sub-specific levels. In the fruit-fly, *Drosophila robusta* Sturtevant, Carson and Stalker (1946, 1947) have made a survey of the geographical variation in the salivary gland chromosomes. The present paper deals with a study of the variation in the morphology of the same species.

HISTORICAL

Among the earliest outstanding studies of geographical variation in insects is that of Goldschmidt (review, 1934). This author studied strains of *Lymantria dispar*, the gypsy moth, from localities in Europe, Asia, and North America, and reared adults in the laboratory under uniform conditions. It was possible, therefore, to attribute the interstrain variability, which was observed and studied genetically, to strain differences in genotype, rather than to the direct effect of the environment. In Japan and Korea, Goldschmidt found geographical gradients or clines in regard to: "strength" of the sex races, chromosome size, incubation period of the eggs, and degree of larval pigmentation. Attempts to correlate these characteristics with the meteorological conditions at the various collecting stations were unsuccessful, although the clines agreed in a general way with the climatic changes from northern to southwestern Japan.

Dobzhansky (1933) studied the geographical variation in the elytral pigmentation of several species of ladybird beetles (Coccinellidae) in which he followed both the general pattern of pigmentation and the size of the spots. Clines were found for both of these characters. In a general way, these findings agreed with Gloger's Rule which states that lightly pigmented forms occur in arid regions and more heavily pigmented forms in humid regions. There is considerable evidence that the major part of the observed variation was based on the genotype.

Alpatov (1929) made a biometrical study of geographical variation in the honey bee in Asia and North America. He found that in Asiatic populations absolute body size, relative size of wax-gland surface, color of abdomen, length of tongue and relative length of legs show clear north-south clines on the Russian plains. These clines tend to be reversed in the Caucasus for the first three characteristics mentioned. Colonies transplanted to different parts of North America retained their morphological identity under the new environmental conditions, and hence Alpatov concluded that the differences he had observed were genetic, rather than directly due to the environment.

Krumbiegel (1932) found that the European races of the beetle, *Carabus*

nemoralis, showed a correlation between observed temperature tolerance and average temperature of the source locality of the race.

The same author (1936) studied geographical variation in the morphology of several species of *Carabus* by measuring museum specimens. He found clines for the relative length of the legs and antennae, with both of these organs becoming relatively shorter in the north. The morphology of the individuals from various localities showed some correlation with the average annual temperature of the source locality. The specimens studied, however, developed in nature under what were probably very diverse environmental conditions, a fact that makes it impossible to say what part of the variation was due to genetic differences, and what part directly due to environment.

In the genus *Drosophila* Timofeeff-Ressovsky (1933) has measured the relative viability of different strains of *D. funebris* from Europe and Russia, and has shown that the strains from southern localities have a relatively high viability at high temperatures, and a lowered viability at low temperatures; while the strains from northern localities show just the reverse relationships. Dobzhansky (1935) has demonstrated a similar relationship between climate of origin and physiology in the two closely related species *D. pseudoobscura* and *D. persimilis;* in this case the physiological character studied was fecundity at various temperatures.

Few biometric studies on the morphology of wild populations of *Drosophila* have been made. This is partly due to the fact that most of the species are remarkably uniform throughout their range, thus making quantitative morphological comparisons particularly difficult. In the case of *D. pseudoobscura* and *D. persimilis* however, Mather and Dobzhansky (1939) have studied a number of strains of each species in an attempt to find morphological differences between the two. They found slight but statistically significant differences in the number of teeth in the sex-combs of the males and in wing-size. Reed, Williams, and Chadwick (1942) demonstrated that the rate of wing-beat in flight was greater in *D. pseudoobscura* than in *D. persimilis.* This physiological difference was found to be correlated with differences in the ratio of wing-size to thorax-volume.

The brief review given above is by no means comprehensive, particularly in regard to the extra-drosophiline groups, but lists some characteristic examples of the types of geographical variation which have been found in the lower taxonomic categories of insects.

Materials and Methods

Drosophila robusta was felt to have unusual recommendations for a study of geographical variation in morphology since it is easily bred in the laboratory, is fairly abundant in nature, has large salivary gland chromosomes facilitating comparison of cytological and morphological variation, and is a woods species, being rarely associated with human habitations. This last fact would tend to decrease the accidental admixture of populations by man, and should allow relatively discrete geographical races to be built up and maintained. *D. robusta* is found in eastern North America, south to the Gulf of Mexico, north to southern Canada, and as far west as Nebraska. Its distribution and habits are more fully discussed by Carson and Stalker (1947).

The 45 strains of *D. robusta* on which this report is based were collected from 22 widely separated localities which roughly cover the known range of the species except for the southern Atlantic states. In most cases, each strain was descended from a single wild female, either inseminated before capture, or inseminated in the laboratory by a male caught at the same locality and at approximately the same time. Fifteen to twenty pairs of adult flies from each strain were aged at 25.5° C. on several changes of standard cornmeal-agar food for approxi-

mately two weeks, and until the majority of the individuals were mature and breeding. The adults were then transferred to a half-pint culture bottle and allowed to oviposit on a slice of richly-yeasted culture medium on a glass slide. After three days, the food slice was examined under the microscope and larvae transferred from it to several half-pint bottles, each containing a sheet of cleansing tissue and 16 cc. of yeast suspension, 36 larvae being transferred to each rearing bottle. Under such conditions there appears to be little competition for food since the number of larvae may be increased to 60 per bottle before the emerging adults show any decrease in body size. The entire development took place at 25.5° C. When the adults emerged they were transferred to standard food medium and allowed to age for several days, after which they were killed with ether and preserved in alcohol for later measurement.

In the early part of the work morphology at all stages of development was studied in an attempt to find workable characters showing differences between the various localities. No clear differences were found in the eggs, larvae or pupae, nor were any marked differences noted in the time of development from egg to adult. In the adults, careful comparisons were made of: color of thorax, abdomen, testis, face and eyes; size and intensity of wing clouds; number of hairs on ventral abdominal plates; external genitalia of both sexes; length and color of eye pile; number and length of aristal branches; length and width of wings, as well as the usual wing-indices used by Drosophila taxonomists; length of femora and tibiae; number of rows of hairs on anterior tibiae; length of thorax and width of head and cheek. Of these characters the ones which showed workable interlocality differences were length of wing, measured from anterior cross-vein to tip; width of wing, measured at right angles to the long axis through the posterior end of the posterior cross-vein; greatest width of the head; length of the thorax from the most anterior point to the tip of the metascutellum, and length of the fore-femur. Although the length of the middle and hind femora showed clear inter-locality variation, they were highly correlated with the length of the fore-femur, and were therefore not included in the final measurements. There was some evidence that the testis color of southern strains was lighter than that of northern strains, but this difference was so affected by age and so difficult to measure quantitatively that it was not followed further. Preliminary measurements were made on both sexes, but since the male and female showed a high inter-locality correlation, final measurements were made on females only.

For measurement, the preserved adults were placed in water for a few minutes, then transferred to a microscope slide, there the head was removed and the rest of the body placed in such a position that the thorax could be seen directly from the side. After the surface film of water had evaporated, thorax-length and head-width were determined. The wing and fore-femora were then dissected off and mounted under a coverslip in water for measurement. One femur was measured on each fly. All measurements were made with the aid of an ocular micrometer in which one unit of measurement equals 483 micra. The mean measurements in the tables and graphs are expressed in these ocular micrometer units, and are based on 35 females from each of the 45 strains.

The strain means and standard errors for the five characteristics mentioned above are listed in table 1. Attempts were made to correlate these means with latitude, longitude, distance from supposed centers of distribution and general ecology, including temperature and humidity of the regions from which the strains originated. Of these, only latitude, average July temperature, and average annual temperature seemed to show suggestive correlations. Figures 1A, B, C; 2A, B show the five sets of strain

TABLE 1. *Average annual temperature and strain means for 22 localities*

Errors listed are standard errors of means

Locality and strain	Aver. annual temp. F.	Thorax length	Head width	Femur length	Wing length	Wing width	Wing length adjusted	Discriminant D_1*	Discriminant D_2*
Big Fish L., Minn.	40.0	2.996 ±0.0071	2.443 ±0.0060	1.543 ±0.0049	4.721 ±0.0120	3.066 ±0.0072	4.803 ±0.0260	0.242	0.648
Rochester, N. Y.	48.0	3.007 ±0.0083	2.421 ±0.0062	1.565 ±0.0052	4.469 ±0.0171	2.920 ±0.0107	4.540 ±0.0338	0.101	0.671
C. S. Harbor, N. Y.	51.0	3.098 ±0.0093	2.484 ±0.0053	1.598 ±0.0048	4.652 ±0.0173	3.074 ±0.0091	4.636 ±0.0130	0.120	0.704
Mt. Vernon, Iowa 1	48.2	3.105 ±0.0062	2.482 ±0.0065	1.595 ±0.0052	4.649 ±0.0139	3.091 ±0.0090	4.626 ±0.0151	0.109	0.711
Mt. Vernon, Iowa 5		3.043 ±0.0080	2.451 ±0.0074	1.567 ±0.0055	4.543 ±0.0184	3.021 ±0.0100	4.580 ±0.0208	0.082	0.676
Mt. Vernon, Iowa 8		3.101 ±0.0099	2.497 ±0.0085	1.603 ±0.0043	4.711 ±0.0139	3.123 ±0.0120	4.693 ±0.0119	0.135	0.704
Mt. Vernon, Iowa 10		3.006 ±0.0084	2.425 ±0.0108	1.545 ±0.0056	4.529 ±0.0147	2.996 ±0.0084	4.600 ±0.0228	0.111	0.661
Mt. Vernon, Iowa 11		3.093 ±0.0080	2.476 ±0.0070	1.578 ±0.0052	4.624 ±0.0133	3.017 ±0.0092	4.613 ±0.0131	0.141	0.679
Glenellyn, Ill.	49.0	3.024 ±0.0079	2.412 ±0.0053	1.573 ±0.0047	4.561 ±0.0147	2.993 ±0.0099	4.616 ±0.0141	0.151	0.726
New Wilmington, Pa.	50.0	3.026 ±0.0092	2.432 ±0.0062	1.571 ±0.0040	4.495 ±0.0143	2.944 ±0.0093	4.548 ±0.0195	0.100	0.677
Philadelphia, Pa.	52.6	3.097 ±0.0076	2.481 ±0.0060	1.594 ±0.0038	4.675 ±0.0125	3.039 ±0.0108	4.660 ±0.0118	0.170	0.696
Wooster, Ohio 42	50.0	3.090 ±0.0100	2.479 ±0.0057	1.580 ±0.0041	4.557 ±0.0188	3.044 ±0.0122	4.548 ±0.0164	0.054	0.682
Wooster, Ohio 47		3.058 ±0.0093	2.473 ±0.0066	1.580 ±0.0051	4.589 ±0.0132	3.036 ±0.0095	4.611 ±0.0137	0.096	0.671
Wooster, Ohio 50		3.018 ±0.0086	2.443 ±0.0067	1.556 ±0.0056	4.541 ±0.0135	3.016 ±0.0099	4.601 ±0.0204	0.092	0.661
Wooster, Ohio 53		3.107 ±0.0082	2.493 ±0.0052	1.590 ±0.0040	4.678 ±0.0110	3.030 ±0.0085	4.654 ±0.0122	0.169	0.680
Cape May, N. J. 1	55.0	3.073 ±0.0061	2.496 ±0.0059	1.577 ±0.0045	4.628 ±0.0126	3.063 ±0.0114	4.636 ±0.0107	0.098	0.652
Cape May, N. J. 2		3.105 ±0.0077	2.497 ±0.0071	1.550 ±0.0044	4.576 ±0.0164	3.051 ±0.0112	4.554 ±0.0164	0.058	0.638
Gatlinburg, Tenn. 1	55.0	3.036 ±0.0105	2.434 ±0.0075	1.563 ±0.0058	4.591 ±0.0163	3.081 ±0.0121	4.634 ±0.0140	0.105	0.702
Gatlinburg, Tenn. 2		3.126 ±0.0092	2.519 ±0.0074	1.576 ±0.0049	4.612 ±0.0152	3.031 ±0.0095	4.570 ±0.0169	0.083	0.642
Gatlinburg, Tenn. 3		3.101 ±0.0067	2.525 ±0.0070	1.571 ±0.0037	4.641 ±0.0120	3.205 ±0.0091	4.623 ±0.0131	−0.007	0.655
St. Louis, Mo. 2	55.0	3.068 ±0.0083	2.464 ±0.0060	1.571 ±0.0057	4.579 ±0.0145	3.060 ±0.0097	4.592 ±0.0095	0.080	0.684
St. Louis, Mo. 550		3.104 ±0.0108	2.498 ±0.0079	1.597 ±0.0047	4.667 ±0.0169	3.090 ±0.0123	4.646 ±0.0141	0.114	0.692
St. Louis, Mo. 792		3.089 ±0.0097	2.493 ±0.0075	1.581 ±0.0049	4.655 ±0.0150	3.084 ±0.0115	4.648 ±0.0123	0.113	0.673
St. Clair, Mo.	55.0	3.051 ±0.0105	2.435 ±0.0081	1.546 ±0.0080	4.541 ±0.0190	3.051 ±0.0106	4.571 ±0.0186	0.078	0.684
Montauk, Mo. 1	57.5	3.113 ±0.0117	2.503 ±0.0097	1.582 ±0.0067	4.571 ±0.0173	3.090 ±0.0168	4.541 ±0.0169	0.017	0.675
Montauk, Mo. 8		3.077 ±0.0097	2.475 ±0.0112	1.595 ±0.0061	4.744 ±0.0111	3.095 ±0.0104	4.748 ±0.0092	0.207	0.707
Montauk, Mo. 13		3.106 ±0.0069	2.501 ±0.0057	1.595 ±0.0040	4.755 ±0.0185	3.156 ±0.0092	4.732 ±0.0210	0.155	0.702
Montauk, Mo. 17		3.136 ±0.0080	2.527 ±0.0067	1.606 ±0.0064	4.676 ±0.0166	3.158 ±0.0089	4.624 ±0.0177	0.050	0.695
Clinton, Ky.	60.0	3.114 ±0.0077	2.518 ±0.0058	1.593 ±0.0051	4.640 ±0.0155	3.116 ±0.0083	4.610 ±0.0147	0.051	0.673
Morrillton, Ark. 8	61.0	3.168 ±0.0109	2.539 ±0.0092	1.599 ±0.0048	4.481 ±0.0192	3.020 ±0.0101	4.399 ±0.0298	−0.063	0.658
Morrillton, Ark. 9		3.127 ±0.0086	2.537 ±0.0056	1.583 ±0.0053	4.515 ±0.0175	3.020 ±0.0130	4.472 ±0.0220	−0.024	0.625
University, Ala.	63.5	3.107 ±0.0091	2.541 ±0.0081	1.579 ±0.0059	4.577 ±0.0177	3.077 ±0.0126	4.553 ±0.0179	−0.003	0.617
Verbena, Ala.	64.5	3.051 ±0.0120	2.499 ±0.0099	1.563 ±0.0058	4.519 ±0.0196	3.009 ±0.0118	4.549 ±0.0187	0.025	0.611
Abbeville, Ala. 19D	66.0	3.091 ±0.0089	2.535 ±0.0074	1.562 ±0.0051	4.501 ±0.0176	3.032 ±0.0098	4.492 ±0.0173	−0.040	0.591
Abbeville, Ala. 19H		3.095 ±0.0100	2.508 ±0.0060	1.549 ±0.0059	4.417 ±0.0185	2.996 ±0.0130	4.404 ±0.0126	−0.075	0.605
Abbeville, Ala. 19K		3.074 ±0.0103	2.500 ±0.0054	1.544 ±0.0065	4.536 ±0.0164	3.007 ±0.0108	4.544 ±0.0136	0.045	0.603
Abbeville, Ala. 19M		3.067 ±0.0133	2.513 ±0.0011	1.546 ±0.0084	4.403 ±0.0227	3.009 ±0.0149	4.417 ±0.0148	−0.100	0.585
Leary, Ga. 21G	66.3	3.114 ±0.0079	2.523 ±0.0050	1.575 ±0.0045	4.459 ±0.0157	3.077 ±0.0118	4.428 ±0.0161	−0.104	0.640
Leary, Ga. 21H		3.066 ±0.0097	2.459 ±0.0066	1.551 ±0.0055	4.513 ±0.0230	2.950 ±0.0119	4.528 ±0.0209	0.095	0.646
Leary, Ga. 21P		3.101 ±0.0060	2.514 ±0.0051	1.537 ±0.0052	4.514 ±0.0182	2.963 ±0.0113	4.496 ±0.0205	0.042	0.581
Leary, Ga. 21V		3.069 ±0.0079	2.514 ±0.0043	1.526 ±0.0047	4.565 ±0.0199	3.008 ±0.0119	4.577 ±0.0173	0.065	0.565
Thomasville, Ga.	67.5	3.098 ±0.0072	2.548 ±0.0062	1.573 ±0.0054	4.436 ±0.0166	2.981 ±0.0100	4.420 ±0.0128	−0.086	0.577
Marshall, Texas	65.4	3.146 ±0.0065	2.561 ±0.0055	1.569 ±0.0044	4.479 ±0.0208	3.015 ±0.0127	4.418 ±0.0375	−0.075	0.589
Austin, Texas 9	69.0	3.026 ±0.0076	2.477 ±0.0033	1.537 ±0.0064	4.389 ±0.0197	2.941 ±0.0147	4.442 ±0.0164	−0.036	0.586
Austin, Texas 10		3.111 ±0.0072	2.522 ±0.0053	1.548 ±0.0052	4.567 ±0.0104	3.024 ±0.0082	4.539 ±0.0117	0.046	0.601

* See text.

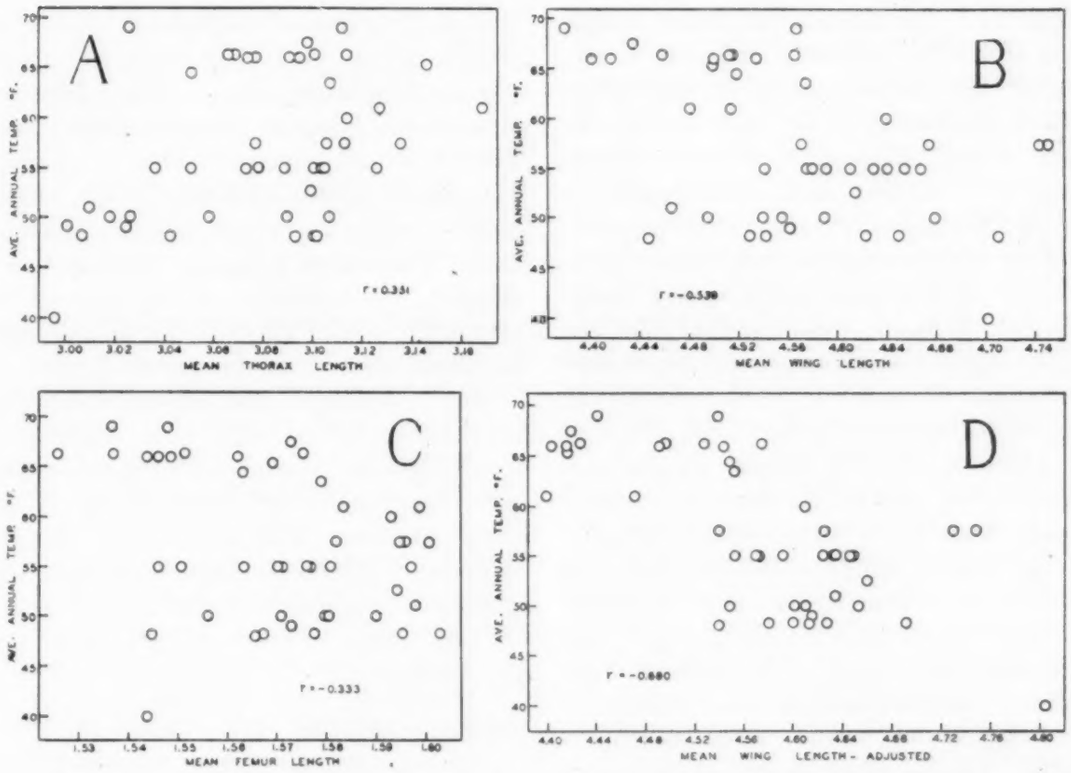

FIG. 1. Strain mean measurements plotted against average annual temperature of locality. A. Thorax-length. B. Wing-length. C. Femur-length. D. Wing-length adjusted to thorax-length. (See text.)

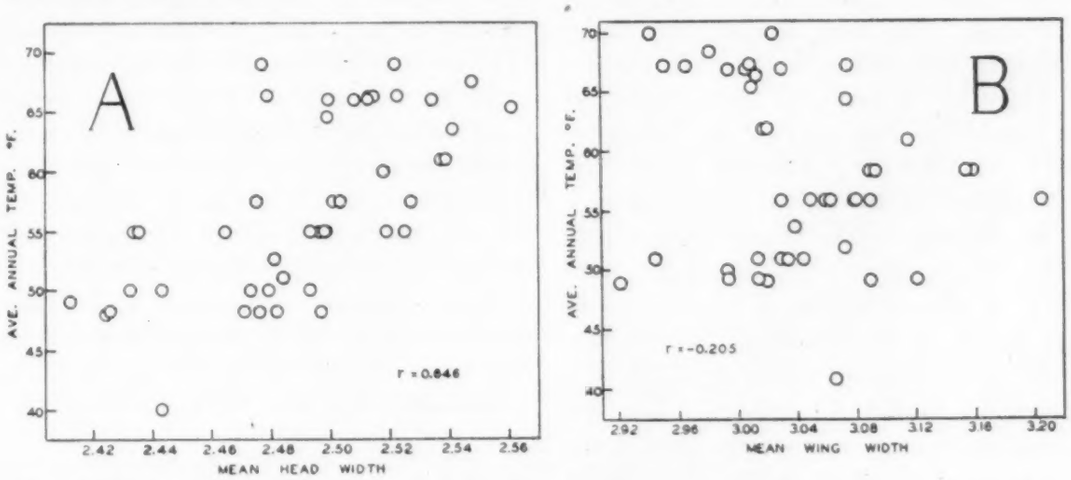

FIG. 2. Strain mean measurements plotted against average annual temperature of locality. A. Head-width. B. Wing-width.

means plotted against average annual temperature (Fahrenheit) of the strain locality. It should be emphasized that all flies measured were raised at the same temperature, 25.5° C. The temperatures used in these graphs are given in the second column of table 1 and come from the U.S.D.A. Yearbook (1941). Correlation coefficients are given in each figure. Of the five characteristics, wing-width, for which $r = -0.205$, shows the lowest correlation with temperature. This is not a significant correlation since it is much smaller than the correlation coefficient at the 5 per cent level of significance, ($r = 0.301$). The coefficients for thorax-

length ($r = 0.351$) and for femur-length ($r = -0.333$) probably indicate a significant correlation of these characters with temperature, since both exceed the value 0.301 mentioned above. Head-width ($r = 0.646$) and wing-length ($r = -0.539$) show a very significant correlation with average annual temperature.

Thus, on the basis of these five measurements alone, it would appear that the strains studied do show graded differences in absolute dimensions correlated with the climate. Individuals from cold climates are characterized by longer wings, narrower heads, shorter thoraces and longer femora than those from warm climates.

The positive temperature correlation in the case of thorax-length, and the negative one in the case of wing-length are especially interesting. The opposite sign of these coefficients indicates a change in the wing/thorax ratio from north to south. This is more clearly shown by a statistical adjustment of strain mean wing-length to the over-all mean thorax-length (3.0818) for the total sample of 45 strains. The method used in making such an adjustment is described by Snedecor (1946). In our case the adjustment was made by the use of the formula: $Y = \bar{y} - 0.9506\ (\bar{x} - 3.0818)$, where Y is the adjusted strain mean wing-length, $\bar{y}$ the unadjusted strain mean wing-length, $\bar{x}$ the strain mean thorax-length, and 0.9506 is the coefficient of regression of wing-length on thorax-length, which represents an average of the wing-on-thorax regressions of the 45 strains. The use of such an average is probably valid, since an analysis of variance (table 2) indicates that the regression coefficients of the 45 strains do not give clear evidence of significant heterogeneity. The adjusted strain mean wing-lengths and their standard errors are given in table 1. Figure 1D shows these adjusted strain means plotted against average annual temperature. They show a highly significant correlation, $r = -0.680$. Thus with an increasingly colder climate, the wing-length increases relative to the thorax-length.

Reed, Williams, and Chadwick (1942) in their study of wing-beat noted that low wing-beat frequencies were associated with species having a high value of the ratio between wing-area and thorax-volume. Conversely high wing-beat frequency was associated with a lower value of this ratio. These authors developed the formula:

$$(\text{wing-frequency})^2 = k\ [\text{muscle volume}/(\text{wing area})\ (\text{wing-length})^3]$$

and tested the relationship by measurements on 11 species of *Drosophila*, using the product of thorax-length, width and depth as an index of muscle volume. The strains and species agreed very well with the theoretical thorax-wing dimension relationship. Frequency of wing-beat, moreover, was shown to differ significantly in the three species, *D. miranda*, *D. pseudoobscura*, and *D. persimilis*. Although these authors found no clear correlation between wing-beat and habitat *within* each of the three species, a correlation was found when the species were considered as units. Thus:

". . . taking the averages for the three groups, we get a strong relationship between habitat

TABLE 2. *Analysis of errors of estimate from average regression of wing-length on thorax-length within strains*

Source of variation	d.f.	Error sum of squares	Mean square
Deviation from average regression within strains	1529	10.5309	
Deviation from individual strain regressions	1485	10.1361	0.006826
Differences among strain regressions	44	0.3948	0.008973

$F = 0.008973/0.006826 = 1.31$ ($F = 1.36$ at 5 per cent level of significance)

and wing-beat frequency. It is known from the early work of Dobzhansky (1937) that *D. miranda* prefers a colder climate than Race B (*D. persimilis*), and that Race B does best at a lower temperature than the optimum for Race A (*D. pseudoobscura*). This ecological relationship is in perfect agreement with the wing-beat frequency, which increases markedly with the optimum temperature progression from *D. miranda* through Race B through Race A."

Thus it appears that for these three closely related forms, species from colder habitats have a high wing/thorax ratio and a low wing-beat frequency, while those from warmer climates are just the reverse.

In our data, although we do not have direct measurements of wing-area, its general trend may be estimated from wing-length and -width data. It will be recalled that wing-length shows a graded increase from south to north. The correlation coefficient for wing-width of -0.205 (figure 2B) indicates that this characteristic either shows no climatic trend, or else shows a slight increase toward the north, similar to that of wing-length. Thus the south to north increase in the proportion of wing-length to thorax-length (figure 1D) must also involve a graded increase in the proportion of *wing-area* to thorax-length. To summarize, we may conclude that a gradient in the proportion of wing-length and area to thorax-length exists, with the wing relatively larger in the northern part of the range.

Any attempt to correlate our data with those of Reed, Williams, and Chadwick should take into account not only thorax-length, but also volume. Does the gradient indicated above for wing-size and thorax-length hold for thorax-volume as well? In the absence of differences in thorax-shape between northern and southern strains a change in any one linear dimension would represent a corresponding change in volume. Measurements of thorax-width and depth are difficult to make on preserved material, however careful observation has failed to reveal any differences in thorax-shape throughout the range of the species. Thus it seems highly probable that we have here the same phenomenon which the above authors observed, although on a lower taxonomic level. Whereas they observed correlation between climate and wing/thorax proportions between species, we have observed it *within* a single species.

It would be expected that if the body-weight of wild flies from various localities were the same, then since for an individual fly the wing-beat frequency is lower at lower temperatures, the larger wing-size of the northern flies would be required to maintain them in the air. However, at present we know neither the average body-weight nor wing/thorax ratio of flies grown in nature, and such information is difficult to obtain since there is great variation in these characteristics both within and between seasons. In the absence of such data, the adaptive significance of the correlation of wing-beat, wing-size, and climate is not entirely clear.

Compound Measurements of the 45 Strains

It will be noted from table 1 and figures 1 and 2 that at least four of the five characters, plus a compound of two of them (wing-length and thorax-length), show significant differences, of an orderly sort, between the northern and southern strains. In order to get an over-all indication of the north-south cline in morphology, a compound measurement which includes all five basic characters is desirable. In devising such a compound two precautions should be taken. First, if the compound is devised to discriminate between certain groups, those characters which have a high intragroup correlation should be given relatively little weight, since they do not give independent evidence in making a separation between groups. Secondly, if the compound measurement is to be as efficient as possible, those characters in which the intergroup variance is large relative to the intra-group variance should be given most weight. The Discriminant Function, developed by Fisher

(1936), fulfills these requirements. It may take the form:

$$D = c_1x + c_2y + c_3z + c_4u + c_5v,$$

where D is the compound measurement, and x, y, z, u and v represent the measurements of the five characters mentioned above, with $c_1 \ldots c_5$ chosen so as to maximize the inter-group variance relative to the intra-group variance. The calculation of such coefficients is discussed by Barnard (1935) and Fisher (1936). To obtain our first discriminant, coefficients were chosen so as to maximize the variance between strains relative to the variance within strains. The coefficients obtained were as follows:

thorax-length	$c_1 = +0.0010$
head-width	$c_2 = -0.8807$
femur-length	$c_3 = -0.2045$
wing-width	$c_4 = -0.6571$
wing-length	$c_5 = +1.0000$

The mean compound measurement, or discriminant D_1, was calculated for each strain by multiplying the strain means for the five characters by their corresponding coefficients, and summing the five products. The discriminants so calculated are listed in table 1 under the column heading D_1.

Attempts were made to correlate the 45 discriminants with latitude, longitude, etc., as in the case of the five basic measurements. With this discriminant as with the basic measurements, the clearest correlation was shown with average annual temperature. The temperature correlation coefficient is -0.701, which is higher than that obtained by considering any one of the five basic measurements or the wing-thorax compound independently.

The discriminant D_1 mentioned above was not chosen so as to discriminate most efficiently between temperature zones or localities, but rather to discriminate between *all* strains, even those in the same zone or locality. On the basis of the high correlation with temperature that this discriminant showed, it was decided to calculate a new and more efficient discriminant, with coefficients so chosen that they would maximize the variance between temperature zones relative to that within temperature zones. For this purpose the 45 strains were arbitrarily assigned to seven zones. The zones contained from two to eleven strains each; the range of the average annual temperature within zones varied from one to eight degrees Fahrenheit. The most efficient coefficients for discriminating between these seven temperature zones turned out to be:

thorax-length	$c_1 = +0.5030$
head-width	$c_2 = -1.2630$
femur-length	$c_3 = +1.0000$
wing-width	$c_4 = +0.2193$
wing-length	$c_5 = +0.0023$

Using these coefficients, and by the method outlined above, a new mean discriminant, D_2, was calculated for each strain. These new discriminants are listed in the last column of table 1. Figure 3 shows D_2 plotted against average annual temperature. In this figure those localities from which more than one strain was measured are represented by the mean of the several strains. The small single circles represent localities from which only one strain was measured, the large single circles represent localities with two or three strains, the symbols consisting of two concentric circles indicate localities from which four or five strains were measured. The letters in the circles refer to the locality key at the bottom of the figure. It will be noted that when this new discriminant is employed the various localities show a striking correlation with average annual temperature. The coefficient of correlation (based on strain means rather than locality means) is now -0.753. Although this is a higher correlation than was obtained by any other single character or combination of characters, it is interesting to note that the wing-thorax compound (with a coefficient of -0.680) shows almost as high a temperature correlation.

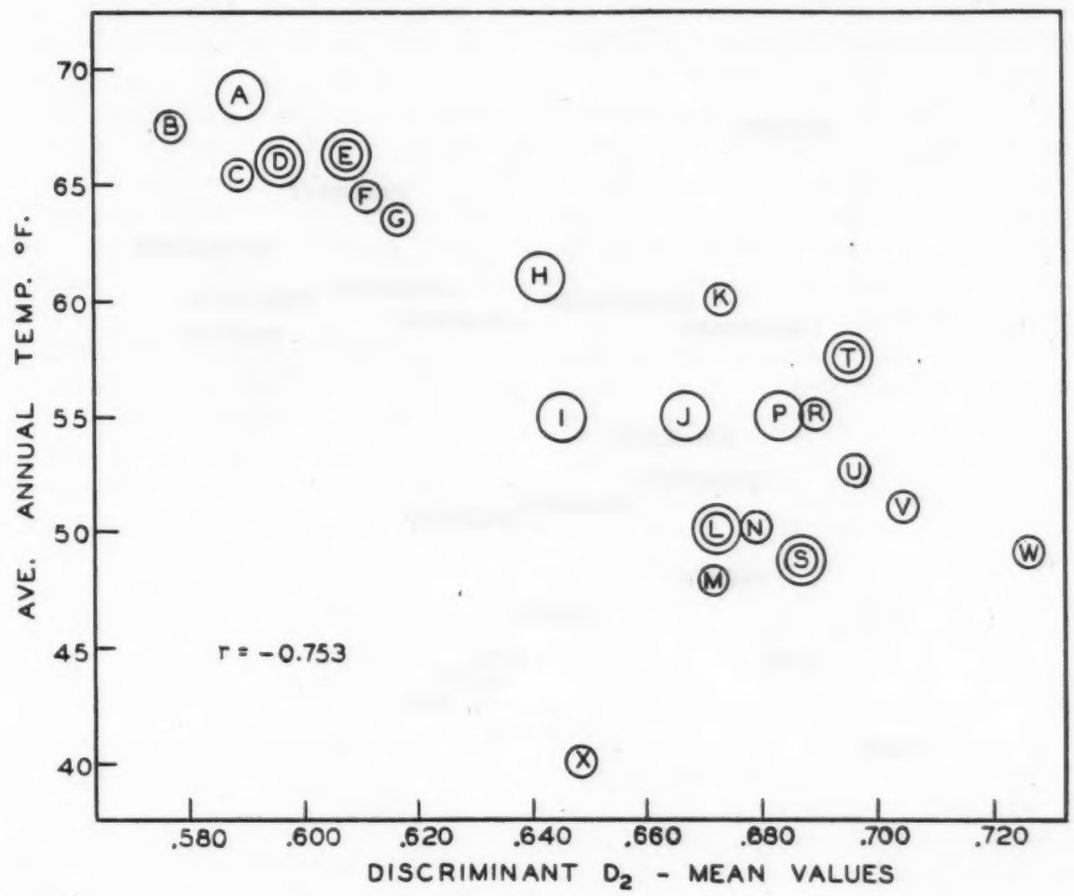

FIG. 3. Locality mean discriminant (D_2) plotted against average annual temperature of locality. Small single circles represent localities with only one strain, large single circles localities with 2–3 strains, two concentric circles represent localities with 4–5 strains. Letters in circles refer to locality key below.

A	Austin, Tex.	L	Wooster, Ohio
B	Thomasville, Ga.	M	Rochester, N. Y.
C	Marshall, Tex.	N	New Wilmington, Pa.
D	Abbeville, Ala.	P	St. Louis, Mo.
E	Leary, Ga.	R	St. Clair, Mo.
F	Verbena, Ala.	S	Mt. Vernon, Iowa
G	University, Ala.	T	Montauk, Mo.
H	Morrillton, Ark.	U	Philadelphia, Pa.
I	Cape May, N. J.	V	C. S. Harbor, N. Y.
J	Gatlinburg, Tenn.	W	Glenellyn, Ill.
K	Clinton, Ky.	X	Big Fish L., Minn.

Figure 4 shows the geographical variation of D_2. In this figure the length of the bars is proportional to $D_2 - 0.52$. It will be noted from this figure and figure 3 that the gradient in over-all morphology, while quite regular in the southern parts of the range, shows a tendency to flatten out north of Missouri and Tennessee.

VARIABILITY BETWEEN STRAINS FROM THE SAME LOCALITY

Table 1 and figures 1, 2, and 3 show that although there is a distinct temperature trend in some of the five basic characters, the wing-thorax compound, and the discriminants D_1 and D_2, there may be considerable variability in strain means

FIG. 4. Geographical variation in strain mean discriminant D_2. Length of bars is proportional to strain mean $D_2 - 0.52$. (See text.)

within any one locality. In fact for all measurements, including the discriminants, there is much overlapping between localities and regions. We will next consider whether this observed variability within localities is significant, and thus due to genotypic differences in the strains, or is merely the result of sampling errors. For such an analysis we have available ten widely separated localities with more than one strain each (table 1) and a total of 33 strains and 1155 flies. Table 3 shows the results of an analysis of variance for each of the five basic measure-

TABLE 3. *Analysis of variance of five basic measurements within localities.* 10 localities; 33 strains, 35 flies measured in each strain.

Source of variation	d.f.	Mean squares				
		Thorax length	Head width	Femur length	Wing length	Wing width
Within strains	1122	0.00285	0.00190	0.00100	0.00281	0.00435
Between strains within locality	23	0.03957	0.02446	0.05923	0.02540	0.07168
Variance ratio, F.		13.884	12.874	59.230	9.039	16.478

F value at 0.01 level of significance = < 1.89

ments. The variance ratios (F) given in the last line of the table are all much higher than the F value at the 5 per cent limit of significance, indicating that the strains within localities are significantly different in respect to each of the five basic measurements. Thus, in the case of these basic measurements, as well as the discriminants derived from them, it is clear that a single strain gives rather limited information on the average genotype of the locality from which it came. Such single strain measurements, while of limited value as representatives of particular localities, when lumped together do give information concerning the general region in which the various localities are found.

The unexpectedly low value of D_2 in the sample from Big Fish Lake, Minnesota, may well be due to the fact that this sample consists of a single strain.

Comparison of Morphological and Cytological Variation

Carson and Stalker (1947) have shown that for many of the known gene arrangements in *D. robusta* there exist clear north-south frequency gradients similar to those found in the morphology. Since a chromosome inversion effectively reduces crossing-over in the heterozygote, the genes included in any one inversion tend to remain together, and may in time become different, as a group, from those genes in the homologous chromosome carrying a different gene arrangement. Approximately 50 per cent of the total length of the salivary gland chromosomes of *D. robusta* is involved in inversions. Thus it is reasonable to suppose that some of the genes which are responsible for the complex of morphological differences between northern and southern strains may be included in these inverted chromosome regions. The parallel changes of the gene arrangements and morphology would suggest that arrangements showing a high frequency in the north and a low frequency in the south would carry genes which are predominantly "northern-type," and would produce the large wing, long legs, short thorax and narrow head characteristic of northern strains, while inversions with a reverse gradient would carry predominantly "southern-type" genes. At present this is only an hypothesis and further more exact comparisons between gene arrangements and morphology are needed to confirm or deny it. Such comparisons are in progress.

Although it seems probable that the geographical differences in morphology are the result of an adaptation to climate, this adaptation may be of a very indirect sort. For example, the morphological phenotype itself may be the by-product of some more fundamental physiological adaptation. While annual temperature is the most obvious *detectable* environmental factor which shows correlation with the morphology, the morphology and physiology may be primarily adapted to some other part of the environment, such as type of flora, which in its turn is correlated with temperature. Thus the apparent flattening out of the morphological gradient in the north may well be a reflection of a change in some environmental factor of which we have no knowledge.

Summary

Studies of geographical variation in the morphology of *Drosophila robusta* Sturtevant are described. These studies are based on 45 strains from 22 widely separated localities in the eastern United States. Final measurements were made on 35 females from each strain, raised in the laboratory under uniform conditions. North-south morphological clines involving a significant correlation with average annual temperature of the source locality were found for the following absolute dimensions: length of thorax, width of head, length of fore-femur, and length of wing. The first two dimensions were greatest in the south, the last two greatest in the north. Absolute wing-width showed a tendency to be largest in the north, although its correlation with average annual temperature was not significant.

FIG. 4. Geographical variation in strain mean discriminant D_2. Length of bars is proportional to strain mean $D_2 - 0.52$. (See text.)

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Comparison of Morphological and Cytological Variation

Carson and Stalker (1947) have shown that for many of the known gene arrangements in *D. robusta* there exist clear north-south frequency gradients similar to those found in the morphology. Since a chromosome inversion effectively reduces crossing-over in the heterozygote, the genes included in any one inversion tend to remain together, and may in time become different, as a group, from those genes in the homologous chromosome carrying a different gene arrangement. Approximately 50 per cent of the total length of the salivary gland chromosomes of *D. robusta* is involved in inversions. Thus it is reasonable to suppose that some of the genes which are responsible for the complex of morphological differences between northern and southern strains may be included in these inverted chromosome regions. The parallel changes of the gene arrangements and morphology would suggest that arrangements showing a high frequency in the north and a low frequency in the south would carry genes which are predominantly "northern-type," and would produce the large wing, long legs, short thorax and narrow head characteristic of northern strains, while inversions with a reverse gradient would carry predominantly "southern-type" genes. At present this is only an hypothesis and further more exact comparisons between gene arrangements and morphology are needed to confirm or deny it. Such comparisons are in progress.

Although it seems probable that the geographical differences in morphology are the result of an adaptation to climate, this adaptation may be of a very indirect sort. For example, the morphological phenotype itself may be the by-product of some more fundamental physiological adaptation. While annual temperature is the most obvious *detectable* environmental factor which shows correlation with the morphology, the morphology and physiology may be primarily adapted to some other part of the environment, such as type of flora, which in its turn is correlated with temperature. Thus the apparent flattening out of the morphological gradient in the north may well be a reflection of a change in some environmental factor of which we have no knowledge.

Summary

Studies of geographical variation in the morphology of *Drosophila robusta* Sturtevant are described. These studies are based on 45 strains from 22 widely separated localities in the eastern United States. Final measurements were made on 35 females from each strain, raised in the laboratory under uniform conditions. North-south morphological clines involving a significant correlation with average annual temperature of the source locality were found for the following absolute dimensions: length of thorax, width of head, length of fore-femur, and length of wing. The first two dimensions were greatest in the south, the last two greatest in the north. Absolute wing-width showed a tendency to be largest in the north, although its correlation with average annual temperature was not significant.

The relative size of wing to thorax was found to increase toward the north. This finding within one species is in agreement with the findings of Reed, Williams, and Chadwick concerning similar variation between different species of the *Drosophila pseudoobscura* group.

Compound measurements (Fisher's Discriminant Function) were calculated. The first set of discriminants, chosen so as to best differentiate between all strains, showed a highly significant correlation with average annual temperature. The second set, chosen so as to discriminate between seven temperature zones, showed a higher correlation with average annual temperature, and indicated that the morphological cline, while fairly regular from Missouri and Tennessee toward the south, showed a tendency to flatten out from Missouri and Tennessee northward.

The inter-locality differences became clear only when locality means were considered, since there was significant inter-strain variation within localities for all five of the absolute measurements mentioned above. The morphological gradient is paralleled in a general way by similar north-south gradients of inversion frequencies found in this species.

Acknowledgment

We are especially indebted to Dr. D. R. Charles for his helpful criticism and advice concerning the statistical procedures used in this investigation. Valuable collections and donations of material were made by the following: Drs. A. H. Sturtevant, W. P. Spencer, J. T. Patterson, G. B. Mainland, A. V. Beatty, C. P. Oliver, M. D. McCarthy, Lillian Nagel; Mr. Arthur Stupka and Mr. J. N. Stalker.

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Literature Cited

Alpatov, W. W. 1929. Biometrical studies on variation and races of the honey-bee (*Apis mellifera*). Quart. Rev. Biol., **4**: 1–58.

Barnard, M. M. 1935. The secular variations of skull characters in four series of Egyptian skulls. Ann. Eug., **6**: 352–371.

Carson, H. L., and H. D. Stalker. 1946. Chromosome studies on *Drosophila robusta*. Genetics, **31**: 213.

——. 1947. Gene arrangements in natural populations of *Drosophila robusta* Sturtevant. Evolution, **1**: 113–133.

Dobzhansky, Th. 1933. Geographic variation in lady-beetles. Amer. Nat., **67**: 97–126.

——. 1935. Fecundity in *Drosophila pseudoobscura* at different temperatures. J. Exp. Zool., **71**: 449–464.

——. 1937. Genetic nature of species differences. Amer. Nat., **71**: 404–420.

Dobzhansky, Th., and Carl Epling. 1944. Taxonomy, geographic distribution, and ecology of *Drosophila pseudoobscura* and its relatives (with seven figures). Carnegie Inst. Wash. Publ., No. 554: 1–46.

Fisher, R. A. 1936. The use of multiple measurements in taxonomic problems. Ann. Eug., **7**: 179–188.

Goldschmidt, R. 1934. Lymantria. Bibliogr. Genetica, **11**: 1–186.

Krumbiegel, I. 1932. Untersuchungen über physiologische Rassenbildung. Zool. Jahrb. (Syst.), **63**: 183–280.

——. 1936a. Morphologische Untersuchungen über Rassenbildung, ein Beitrag zum Problem der Artbildung und der geographischen Variation. Zool. Jahrb. (Syst.), **68**: 105–178.

——. 1936b. Sinnesphysiologische Untersuchungen an geographischen Rassen. ibid., 179–204.

——. 1936c. Untersuchungen über gleichsinnige geographische Variation. ibid., 481–516.

Mather, K., and Th. Dobzhansky. 1939. Morphological differences between the "races" of *Drosophila pseudoobscura*. Amer. Nat., **73**: 5–25.

Reed, S. C., C. M. Williams, and L. W. Chadwick. 1942. Frequency of wing beat as a character for separating species, races and geographic varieties of Drosophila. Genetics, **27**: 349–361.

Snedecor, G. W. 1946. Statistical methods. (Fourth edition.) The Collegiate Press, Ames, Iowa.

Timofeeff-Ressovsky, N. W. 1933. Über die relative Vitalität von *Drosophila melanogaster* Meigen und *Drosophila funebris* Fabricius unter verschiedenen Zuchtbedingungen, in Zusammenhang mit den Verbreitungsarealen dieser Arten. Arch. Naturgesch. N. F. **2**: 285–290.

U. S. Dept. Agric. 1941. Yearbook of Agriculture: "Climate and Man." U. S. Govt. Printing Office. Washington, D. C.

HYBRIDIZATION BETWEEN THE SUNFLOWER SPECIES *HELIANTHUS ANNUUS* AND *H. PETIOLARIS*

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INTRODUCTION

A study of *Helianthus annuus* was begun by the writer in 1943. The first hybrid swarm of *H. annuus* and *H. petiolaris* was encountered in the summer of 1945, and subsequently two other hybrid swarms were discovered. Although the studies are still being carried on, it seems desirable at the present time to present a preliminary survey of the two species.

This work has included both the collection of specimens in the field and the growing of plants in the greenhouse and in the field. The artificial hybrid between the two species has been produced and analyzed. In addition, cytological studies have been made of the two species and their hybrid.

Herbarium specimens have been consulted from a number of institutions. To the curators of these herbaria the writer wishes to express his thanks. The writer also would like to make acknowledgments to the following: Dr. Edgar Anderson, who first suggested the study of *Helianthus;* the Missouri Botanical Garden for a grant to travel to Arizona; Dr. Harold S. Colton for placing the facilities of the Museum of Northern Arizona at the writer's disposal; and Dorothy Heiser for help with the statistics.

TAXONOMY

Fortunately there are few nomenclatorial difficulties to be dealt with in the treatment of the two species. *Helianthus annuus* was described by Linnaeus in 1753. Of the many synonyms of *H. annuus* only one, *H. aridus* of Rydberg, requires discussion here. Cockerell (1915) thought that *H. aridus* might possibly be a hybrid of *H. annuus* × *H. petiolaris,* but later (1918) after making the artificial cross he concluded that *H. aridus* was a variety of *H. annuus* subsp. *lenticularis.* The New York Botanical Garden was unable to locate the type of *H. aridus* for examination by this writer, but from the description of the species the possibility that it may represent a hybrid derivative of *H. annuus* × *H. petiolaris* should not be ruled out. Six specimens from the New York Botanical Garden annotated by Rydberg as *H. aridus* have been examined and it was found that five of them should be referred to *H. annuus* and one to *H. petiolaris.* From the examination of other herbarium specimens it appears that the name *H. aridus* has served as a pigeon hole for the filing of misfit specimens of *H. annuus* and, to a lesser extent, of *H. petiolaris.* These misfits are either depauperate plants or hybrid derivatives. Hence the writer is unable to give taxonomic recognition to *H. aridus* and suggests that it be placed in synonymy under *H. annuus* as has been done by Watson (1929) and Blake (1942).

Helianthus petiolaris was first described by Nuttall, and its synonymy has been discussed by both Cockerell (1918) and Watson (1929). The variety *canescens* of A. Gray requires mention here. This variety which occurs in the southwestern United States extending into Mexico was raised to specific rank by Wooton and Standley under the name *H. canus* (*H. petiolaris* var. *canus* Britton) and has

been retained as a species by Watson. The chief characteristic separating it from *H. petiolaris* lies in its dense cancescent pubescence. In view of the facts that the pubescence appears to be a variable character and that the two appear to intergrade, judging from the examination of herbarium specimens, it seems best to regard it as merely a variety as has been done by Blake (1942) until experimental studies can be undertaken.

Cockerell's *H. petiolaris* var. *phenax* is a form with yellow disk which, for reasons to be given below, this writer regards as an introgressive type.

No new names have been provided for the hybrids. The F_1 is simply designated as *H. annuus* × *H. petiolaris,* and no attempt has been made to give variety or form names to the many introgressive types which have been encountered in this study.

The literature citations of the species and combinations discussed are given below.

H. annuus L., Sp. Pl. 904. 1753.
H. lenticularis Dougl. in Lindl., Edwards' Bot. Reg., **15**: pl. 1265. 1829.
H. annuus ssp. *lenticularis* Ckll., Science, n. s., **40**: 284. 1914.
H. aridus Rydb., Bull. Torrey Bot. Club, **32**: 127. 1905.

H. petiolaris Nutt., Jour. Acad. Nat. Sci. Phila., **2**: 115. 1821.
H. petiolaris var. *phenax* Ckll., Nature (London), **66**: 174. 1902.

H. petiolaris var. **canescens** A. Gray, Smith. Contr. Knowl. (Pl. Wright., **1**: 108), **3**: 108. 1852.
H. petiolaris var. *canus* Britton, Mem. Torrey Bot. Club, **5**: 334. 1894.
H. canus Wooton and Standley, Contr. U. S. Nat. Herb., **6**: 190. 1913.

Geographical Distribution

Both *H. annuus* and *H. petiolaris* are widespread in North America. Both are common in the western United States and occasional eastward. *Helianthus annuus* is the more widely distributed of the two. The two species are native to North America but any effort to delimit their natural boundaries before the appearance of man and their subsequent spread as weeds meets with little success. Most authors have held that both species are indigenous to the Great Plains region west of the Mississippi River and have since been introduced elsewhere. Both are now rather common in the southwest.

Although both species grow together in a variety of localities there do seem to be some slight ecological preferences. In general, *H. annuus* seems to be more restricted to heavy soils and *H. petiolaris* to sandy soils. Deam (1940) writes concerning *H. petiolaris* in Indiana: "This species has just begun to invade the state. It was first reported in 1905. . . . It grows in very sandy soil and within the area of its distribution in the state where the sand has been disturbed it has become an abundant weed in cities and along roads and railroads." This writer has observed that *H. petiolaris* is more frequent as a weed of railroads and that *H. annuus* is more common in waste places about cities and along roadsides.

The observations of Dr. G. L. Stebbins, Jr. are of interest here. He writes (in litt.) after a trip cross-country: "The most impressive thing to me was the continuous, dense population of both *H. petiolaris* and *H. annuus* extending along the roadside as well as the railroad tracks all of the way from the beginning of the short-grass plains near Cheyenne, Wyoming, to their eastern border in Nebraska. *Helianthus petiolaris* was in full bloom, *H. annuus* not yet out, so the seasonal difference between them was marked, although there must be a good deal of overlap later on. *Helianthus annuus* was apparently only in the more fertile and better watered areas."

The seasonal difference which Stebbins observed in time of blooming is entirely in accord with the writer's observations.

H. petiolaris in most areas comes into bloom in June and *H. annuus* generally not until July. However, both continue to bloom for a rather long period of time, *H. petiolaris* through July into August and *H. annuus* on into September.

Dr. Stebbins and the writer are in agreement that the distributions of the two species were originally allopatric and that they have been brought together through man's interference. Dr. Stebbins goes on to write: ". . . before man came wild *H. annuus* was probably a plant of disturbed soil-bluffs, mud bars, etc.; *H. petiolaris,* on the other hand, may have originated in a dryer climate with a shorter growing season—probably on the high plains of Colorado or Wyoming, along creek bottoms or sandy washes of 'bad land' areas." In view of our present knowledge this hypothesis appears plausible.

Morphology

A detailed discussion of the morphology of the two species is not necessary here because descriptions of both species are given in Watson (1929, p. 351 and p. 357).

The usual many and well defined differences between the species are occasionally bridged by hybrid swarms. However, a high degree of sterility among the intermediates is indicated by a study of seed and pollen fertilities. The introgressants or introgressive forms, those showing the influence of genes from the other species, generally show little or no reduction in

Table 1. *Comparison of artificial F_1 of* Helianthus annuus × H. petiolaris *with parent species from greenhouse plants*

	H. petiolaris (*602*) (5 plants)	Hybrid (*601*) (6 plants)	*H. annuus* (*603*) (5 plants)
Height	.35–.45 m.	.55–.70 m.	.80–.90 m.
Pubescence of stem	glabrate	hispidulous	hispid
Branching	much branched	much branched	little branched
Lower leaves: (fig. 4)			
shape	lanceolate	lanceolate to ovate-lanceolate	lanceolate to ovate-lanceolate
blade length	6.5–8.4 cm.	7.5–10.5 cm.	7.5–9.6 cm.
width	2.0–2.6 cm.	3.3–4.7 cm.	3.2–5.8 cm.
serration	entire or obscurely serrulate	irregularly to regularly serrate	regularly serrate
pubescence	soft	soft	rough
Length of peduncles	5–15 cm.	mostly about 5 cm.	4 cm. or less
Disk diameter	2.3 cm. or less	2.5–2.8 cm.	3.5 cm. or more
Bracts of the involucre: (fig. 4)	gradually attenuate	intermediate	abruptly attenuate
width	3 mm.	4 mm.	7 mm.
pubescence of margin	hispidulous in 4 plants, somewhat hispid in one	approaching that of *H. annuus*	hispid
Chaff: (fig. 4)			
pubescence of middle awns	hairs long	hairs intermediate in length	hairs short
color in age	straw colored	purple	purple
Rays:			
number	13–16	15–21	21–30
length	2.3–2.7 cm.	2.7–3.4 cm.	4.0–4.5 cm.
width	.8– .9 cm.	.9–1.2 cm.	1.3–1.6 cm.
Length of corolla of disk flowers	4.0–5.0 mm.	5.0–6.0 mm.	6.0–6.5 mm.
Achenes:			
length	5 mm.	5–6 mm.	6–7 mm.
width	1.5–2.0 mm.	2.5–3.0 mm.	3 mm.

fertility. In spite of introgression of certain characters from the other species there remains no doubt as to which of the two species these forms should be referred.

It is difficult to define the limits of a normal plant of *H. annuus* and *H. petiolaris*. In both species the phenotype may be greatly modified by the environment. Since both are annuals and weeds this is not surprising. Secondly, both species consist of many genetic races. Table 1 gives a comparison of a single population of each species and the artificial hybrid grown under greenhouse conditions. The plants of both species, particularly *H. annuus*, when grown in pots are much smaller in many respects than those encountered in nature.

The height of the two species does require brief discussion. *Helianthus annuus* is normally from 1.0 to 3.0 meters tall (excluding cultivated forms); *H. petiolaris* is normally about 0.9 meters tall. Watson gives the height of the latter species as 0.4 to 4.0 meters. He mentions finding one individual of *H. petiolaris* four meters tall growing in a colony of *H. annuus*. He writes that such tall plants are occasionally found where *H. petiolaris* grows abundantly and that it would be interesting to know the explanation of the gigantic size "whether it be a mutation or the result of hybridism with *H. annuus*."

The color of the corolla lobes of the disk-flowers of the two species also requires brief explanation. In *H. annuus* the color is generally red or purple although in some populations yellow lobes are quite common. The color of the lobes in *H. petiolaris* is red or purple, although a form with yellow lobes has been described by Cockerell (1902). The writer has found a single plant of *H. petiolaris* in a hybrid swarm which possessed yellow lobes. Except for the color of lobes this latter plant appeared to have all of the characteristics of *H. petiolaris* and was fully fertile.

Cytology

Both *H. annuus* and *H. petiolaris* have the haploid count of seventeen chromosomes. *Helianthus annuus* has been reported with this number by several work-

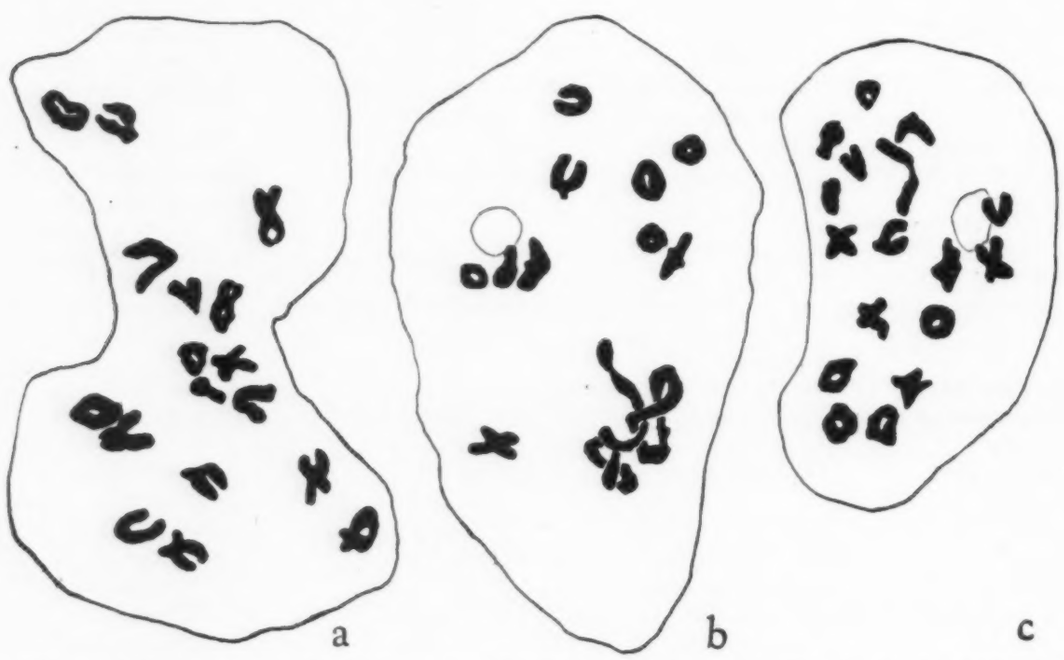

Fig. 1. Camera lucida drawings of chromosomes of *Helianthus annuus*, *H. petiolaris*, and artificial hybrid: (a) *H. annuus* (*752*), seventeen pairs, (b) *H. annuus* × *H. petiolaris* (*781*), ten pairs, two chains, and one ring, (c) *H. petiolaris* (*755*), seventeen pairs. All × 1370.

ers (see Geisler, 1931, for bibliography). This writer has verified the count of seventeen for *H. annuus* from both cultivated and wild material from a number of collections (figure 1, a). *Helianthus petiolaris* is reported here for the first time with seventeen pairs (figure 1, c).

The hybrid between the two species was grown in the greenhouse in Berkeley during the winter of 1945–46. Although no difficulty was experienced in making suitable aceto-carmine smears of the parent species from greenhouse material, great difficulty was encountered in making smears of the hybrids suitable for detailed study. However, it could be ascertained that meiosis did not proceed normally in the hybrid material. Rings and chains of chromosomes were observed at metaphase I and chromatid bridges with acentric fragments at anaphase I. This would tend to indicate that the parent species differ for both translocations and inversions. Meiosis was later studied in fifty cells of a hybrid between cultivated *H. annuus* ("Mammoth Russian") and *H. petiolaris*. In the latter hybrid it was found that there were from 7 to 11 bivalents at metaphase I, an occasional univalent, and that the remainder of the chromosomes were associated in two or three chains or rings of several chromosomes each (figure 1, b).

Analysis and Discussion of Hybrid Swarms and Artificial Hybrids

First hybrid swarm

In the early fall of 1944 a hybrid swarm of *H. annuus* and *H. petiolaris* was found in St. Louis, Mo., near the intersection of Des Peres Avenue and the University street car tracks. The plants which were few in number were mostly depauperate individuals, but several of the plants were obviously morphological intermediates between the two species. Moreover, those plants intermediate in appearance set few if any good seeds. Since these plants were mostly depauperate and do not fit in well with the methods of scoring the other populations no attempt is made in presenting the scoring of this population here. The good seeds from the putative hybrids were planted the following winter but only two germinated. The two plants secured, however, did show segregation for *H. annuus* and *H. petiolaris*-like characters. The first plant (*622–1*) had deeply serrate leaves (figure 4, l), disk-flowers with yellow corolla lobes, and involucral bracts which in shape and pubescence resembled those of *H. petiolaris*. The second plant (*622–2*) had entire leaves (figure 4, k), disk-flowers with purple corolla lobes, and bracts similar to those of *H. annuus*. Both plants possessed less than 20 per cent good pollen and set no seed on crossing.

The next summer this locality was visited again, but unfortunately most of the plants had been mowed down. Of the few plants remaining one was of exceptional interest. This plant, previously mentioned, had over 90 per cent good pollen and fitted the description of *H. petiolaris* except for the yellow lobes of the disk-corollas. One other such plant has been described by Cockerell as *H. petiolaris* var. *phenax*. It is the opinion of the writer that plants of *H. petiolaris* with yellow disk-corolla lobes have probably come about through the introgression of a gene or genes from *H. annuus*.

Second hybrid swarm

After finding the first hybrids between *H. annuus* and *H. petiolaris* the writer reexamined his collections made in the summer of 1944 near Flagstaff, Arizona, where the two species had been found growing in close proximity. One plant (*893*) was found to be more or less intermediate morphologically between the two species and was characterized by low pollen fertility.

A second trip was made to Arizona in the late summer of 1945 with the purpose of examining the sunflowers more critically. The trip was rewarded by the finding of a large hybrid swarm by the roadside near the Museum of Northern

Arizona, north of Flagstaff. Sixty-six plants were scored in the field for leaf width and margin, width of the involucral bracts, disk diameter, and pubescence of the chaff. Since it was late in the season the rays were not in suitable condition for scoring. The characters scored were assigned values following the method of Anderson (1936). Characters which were *H. annuus*-like were assigned a value of 2, those which were like *H. petiolaris* were assigned a value of 0, and any intermediate condition was given a value of 1. The resulting histogram showed a distinctly bimodal distribution (figure 2).

Thirty-six plants were collected from the hybrid swarm for a study of pollen and seed fertilities. Pollen counts were made by smearing anthers in lactophenol and cotton blue and those grains which took a dark blue stain were counted as good. The seed fertility was measured by counting the number of filled and unfilled achenes to the head. Those plants with low percentages of good pollen (68 per cent or less) and low seed set (less than 50 per cent) were scored as hybrids or hybrid derivatives. The remainder of the plants were placed with the non-hybrid group. A few plants with as low as 55 per cent good pollen were placed with the latter group since they showed no reduction from the normal seed set. This group of non-hybrids was easily subdivided into two groups depending upon their morphological resemblance to either *H. annuus* (*1642b*) or *H. petiolaris* (*1642a*). Some of the hybrid group (*1642c*) approached either *H. annuus* or *H. petiolaris* rather closely in appearance, but for the most part they were more or less intermediate.

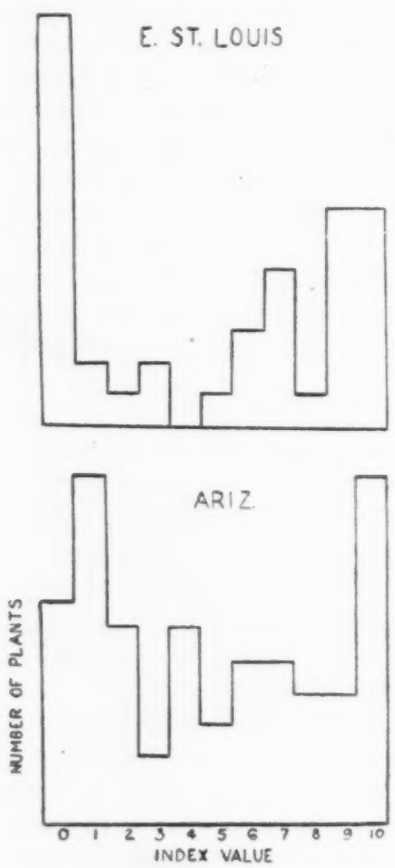

FIG. 2. Histograms of two hybrid swarms of *Helianthus annuus* and *H. petiolaris*. (See text for explanation.)

For most of the characters measured the variability of the group classed as hybrids was greater than that of either parent. The measurements of the disk diameter are presented in table 2. The coefficient of variability of the disk diameter for the plants of *H. annuus* was 14.5, for *H. petiolaris* 9.0, and for the hybrids 16.5.

The great variability of the hybrids can be accounted for if it is assumed that the hybrid swarm is one of several years standing and the hybrid group consists of backcrosses, F_2's, and more complicated crosses, in addition to F_1's. The pollen fertilities tend to bear out this conclusion. The amount of good pollen of the hybrid group ranged from 4 to 68 per cent with a mean of 18 per cent. The plants of both *H. annuus* and *H. petiolaris* also showed rather great ranges of pollen fertility. The percentage of good pollen of *H. annuus* ranged from 55 to 100 per cent with the mean at 81 per cent, that of *H. petiolaris* from 61 to 100 per cent with the mean at 87 per cent.

Seeds were collected from this population but germination was very poor and no attempt will be made here to discuss the few greenhouse plants obtained.

TABLE 2. *Measurements of disk diameter of* Helianthus annuus, H. petiolaris, *and hybrids from Arizona and Illinois*

	Number of plants	Mean	Standard deviation	Coefficient of variability
Flagstaff, Arizona				
H. annuus (*1642b*)	10	3.3	0.48	14.5
H. petiolaris (*1642a*)	13	2.1	0.19	9.0
hybrids (*1642c*)	13	2.3	0.38	16.5
East St. Louis, Illinois				
H. annuus (*1807b*)	17	3.3	0.48	14.5
H. petiolaris (*1807a*)	17	2.3	0.33	14.3
hybrids (*1807c*)	9	2.9	0.29	10.0
H. annuus (*1807d*)	19	3.4	0.29	8.5

Third hybrid swarm

In the summer of 1946 another hybrid swarm was found in the railroad yards along the Mississippi River near Eads Bridge in East St. Louis, Ill. *Helianthus annuus* becomes quite conspicuous in the loam soil along the roadside after one crosses the bridge from St. Louis. The plants of *H. annuus* extend down onto the cindery railroad beds where *H. petiolaris* occurs. Forty-three specimens were taken where the two species came together, and these were tentatively identified as *H. annuus* (*1807b*), *H. petiolaris* (*1807a*), and hybrids (*1807c*). All of these identifications with a single exception were verified upon later examination. The plants identified as *H. annuus* and *H. petiolaris* proved to have high percentages of good pollen (over 90 per cent) and, with the one exception mentioned, the plants determined as hybrids had low percentages of good pollen (less than 30 per cent). Subsequent examination of the one plant which had nearly perfect pollen proved it to be a depauperate plant of *H. annuus*. Watson (1929) has previously commented upon the difficulty of identifying depauperate specimens of annual sunflowers.

In addition to the plants collected from the hybrid swarm a number of plants of *H. annuus* (*1807d*) which were growing nearby along the roadside in loam soil were collected.

The plants of both *H. annuus* and *H. petiolaris* as well as the hybrids differed considerably from the Arizona specimens. These differences are not unexpected inasmuch as both species differ genetically throughout their ranges. The Arizona plants of *H. petiolaris* seemed to show some influence of the southwestern variety, *H. petiolaris* var. *canescens*, in the pubescence of their stems which was lacking in the St. Louis plants. Widely different ecological conditions, of course, would be expected to account for some of the other differences.

The pattern of variability was also different as suggested by the measurements of the disk diameter (table 2). For example, the coefficient of variability of the disk diameter for *H. annuus* (*1807b*) was 14.5, for *H. petiolaris* 14.3, and for the hybrids 10.0. The plants of *H. annuus* from along the roadside showed still less variability; their coefficient of variability for disk diameter was 8.5. The ray size, ray number, width of involucral bracts, and leaf index showed the same general trend of variability as that encountered in the disk diameter.

The possible causes for less variation among the hybrids than among the parents is worthy of consideration. The low variability of the hybrids could be accounted for if all of the hybrids were F_1's. The pollen fertilities of this hybrid group showed the same range of good pollen (0–30 per cent) as did the artificial F_1

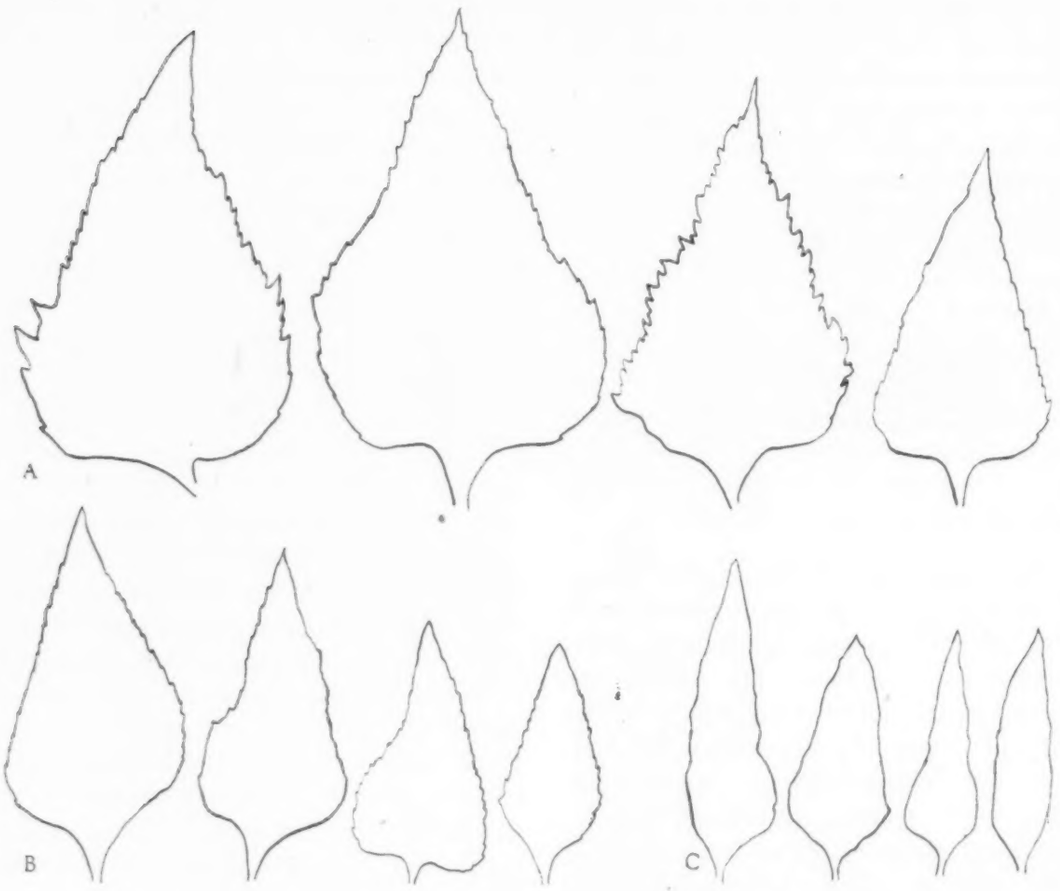

FIG. 3. Leaf tracings from plants of East St. Louis hybrid swarm: (A) *Helianthus annuus* (top), (B) hybrids (lower left), (C) *H. petiolaris* (lower right). × approx. 2/5.

(discussed below) although the mean (20 per cent) for the natural hybrids was slightly higher. However, the morphological variation in the natural hybrids is rather great for F_1's even though the parent stocks may have been highly heterozygous. A second possible explanation is that the hybrids consisted merely of F_1's, possibly F_2's, and first generation back crosses without the more complicated types of backcrosses which were probably present in the Arizona hybrid swarm. This hypothesis is supported by the fact that in the Arizona population it was very difficult to separate the hybrids from the species on the basis of pollen fertility, whereas no such difficulty was encountered with the East St. Louis plants.

The great difference in the variability of the plants of *H. annuus* from along the roadside (*1807d*) and those from the hybrid swarm (*1807b*) is probably due in part to differences in soil conditions as well as to the greater amount of introgression of *H. petiolaris* into the latter (*1807b*).

A histogram for this hybrid swarm utilizing the same characters employed for the Arizona population is presented in figure 2. A number of other histograms were made using characters of the rays, pubescence, and disk-flowers in addition to those previously mentioned. All of the histograms showed a bimodal distribution for the population.

Later in the summer of 1946 achenes were collected from this population, and greenhouse plantings were made the next winter at Davis, California. Progeny of

the hybrid plants again showed some segregation for *H. annuus*- and *H. petiolaris*-like characters.

Artificial F_1

The hybrid between *H. annuus* and *H. petiolaris* was made in the summer of 1945, employing essentially the same technique as that of Putt (1941).[1] The reciprocal cross was made, but the plant of *H. annuus* was injured and did not mature its seeds. The *H. annuus* plant selected was fairly typical of the wild sunflowers from St. Louis except that it possessed some red in its rays. The *H. petiolaris* plant used was from seed of St.

[1] Since that time it has been found that most of the wild annual species of *Helianthus* are rather highly self-sterile, and heads are rubbed in making the crosses instead of employing the more time consuming emasculating and hand pollinating of the individual flowers.

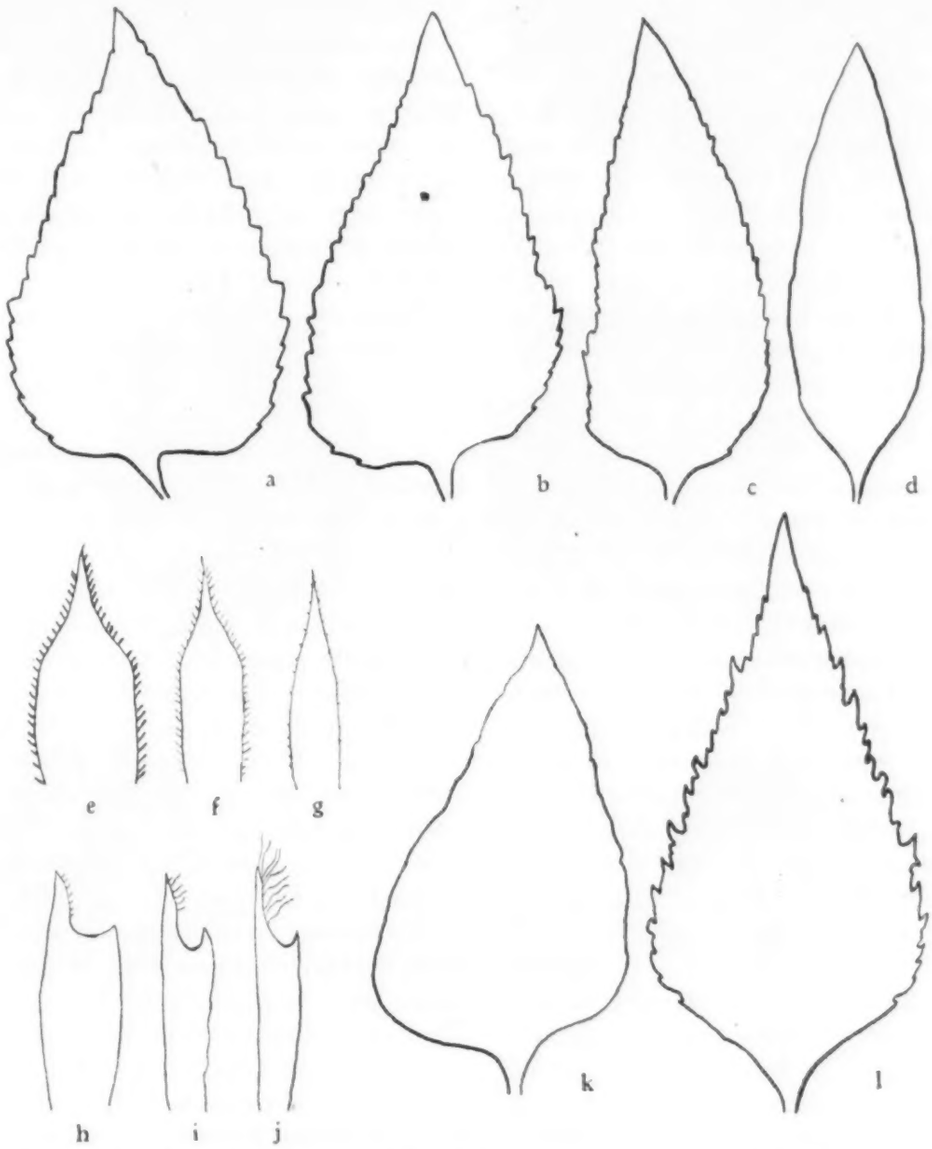

FIG. 4. a–d, Leaf tracings of artificial hybrid and parents, ×⅔: (a) *Helianthus annuus* (*603*), (b, c) F_1 (*601*), (d) *H. petiolaris* (*602*). e–g, Involucral bracts of artificial hybrid and parents, ×2: (e) *H. annuus* (*603*), (f) F_1 (*601*), (g) *H. petiolaris* (*602*). h–j, Chaffy bracts from center of heads of artificial hybrid and parents, ×3⅓: (h) *H. annuus* (*603*), (i) F_1 (*601*), (j) *H. petiolaris* (*602*). k–l, Leaf tracings of progeny of a natural hybrid, ×⅔: (k) no. *622–2*, (l) no. *622–1*.

Louis *H. petiolaris*. A large amount of good seed was obtained from the cross.

The F_1 was grown in the greenhouse at Berkeley, California, during the winter of 1945–46. All of the plants were very vigorous and bloomed much longer than either parent. A comparison of the F_1 with the parent species which were grown at the same time is given in table 1. Drawings of leaves, involucral bracts, and chaff are given in figure 4. Direct size comparisons cannot be made between greenhouse and field populations, but the appearance of the synthetic F_1 lends additional proof to the hypothesis that the putative hybrids are truly of hybrid origin. The F_1 agrees rather closely with that previously described by Cockerell (1918).

The pollen fertilities in the ten F_1 plants were very low, ranging from 0 to 30 per cent good pollen with a mean of 14 per cent. Sister plants were crossed by rubbing heads together, and the seed set was less than 1 per cent.

Artificial F_2

The F_2 consisted of five plants which were grown in the greenhouse at Davis during the winter of 1946–47. No two plants were alike but in general they resembled *H. annuus* more nearly than *H. petiolaris*. However, none of the plants was like *H. annuus* in all particulars. Plant no. *768–3* showed the nearest approach, agreeing with *H. annuus* in seven morphological characters, intermediate in four, and approaching *H. petiolaris* in the pubescence of the chaff. The pollen fertilities varied greatly. The percentages of good pollen for the five plants were 13, 39, 48, 50, and 97 per cent. It appears that it is possible for the sterility barrier to be overcome to some extent in the F_2. A plant similar to the F_2 plant with 97 per cent good pollen if found growing wild would be called an extreme introgressant.

Another interesting feature among the recombinations was the yellow disk-corolla lobes of plant no. *768–2*. Neither of the parent species had yellow disks, although the factor may have been carried in the recessive state in one or the other, probably in *H. annuus*. No attempt will be made to go into the full genetic implications here, but it should be pointed out again that two plants of *H. petiolaris* with yellow disk-corolla lobes have turned up in nature. Thus the evidence from the F_2 offers further support of the hypothesis that the occurrence of the yellow lobes of the disk-corollas in *H. petiolaris* has come about as a result of hybridization with *H. annuus*.

No weakness was observed in the F_2 although progeny of putative natural hybrids growing under the same conditions did show some weakness. Many of the latter plants were dwarfs, and furthermore they were subject to attack by red spider to which the parent species and artificial F_2's were immune.

Backcrosses of the F_1 to the two parents have not yet been grown.

Herbarium studies

A number of herbarium specimens have been consulted in the present study. Both species show a great deal of variability throughout their range, and it is entirely possible that some of this variability could have come about through the introduction of the germ plasm from one of the species to the other. The following characteristics which show up in some herbarium specimens of *H. petiolaris* might have come about through introgression: broad leaves, serrate leaves, hispid involucral bracts, and a general increase in size of all parts of the plant. Similarly, plants of *H. annuus* have been seen which embody certain characteristics which might have been derived from *H. petiolaris*. They are principally as follows: narrow leaves, narrow involucral bracts, smaller disks, densely pubescent chaff, and a reduced number of rays. It is, of course, almost impossible in most cases to judge from herbarium specimens whether the size differences are genetic or merely represent an ecological modification of the phenotype. The writer fully realizes that

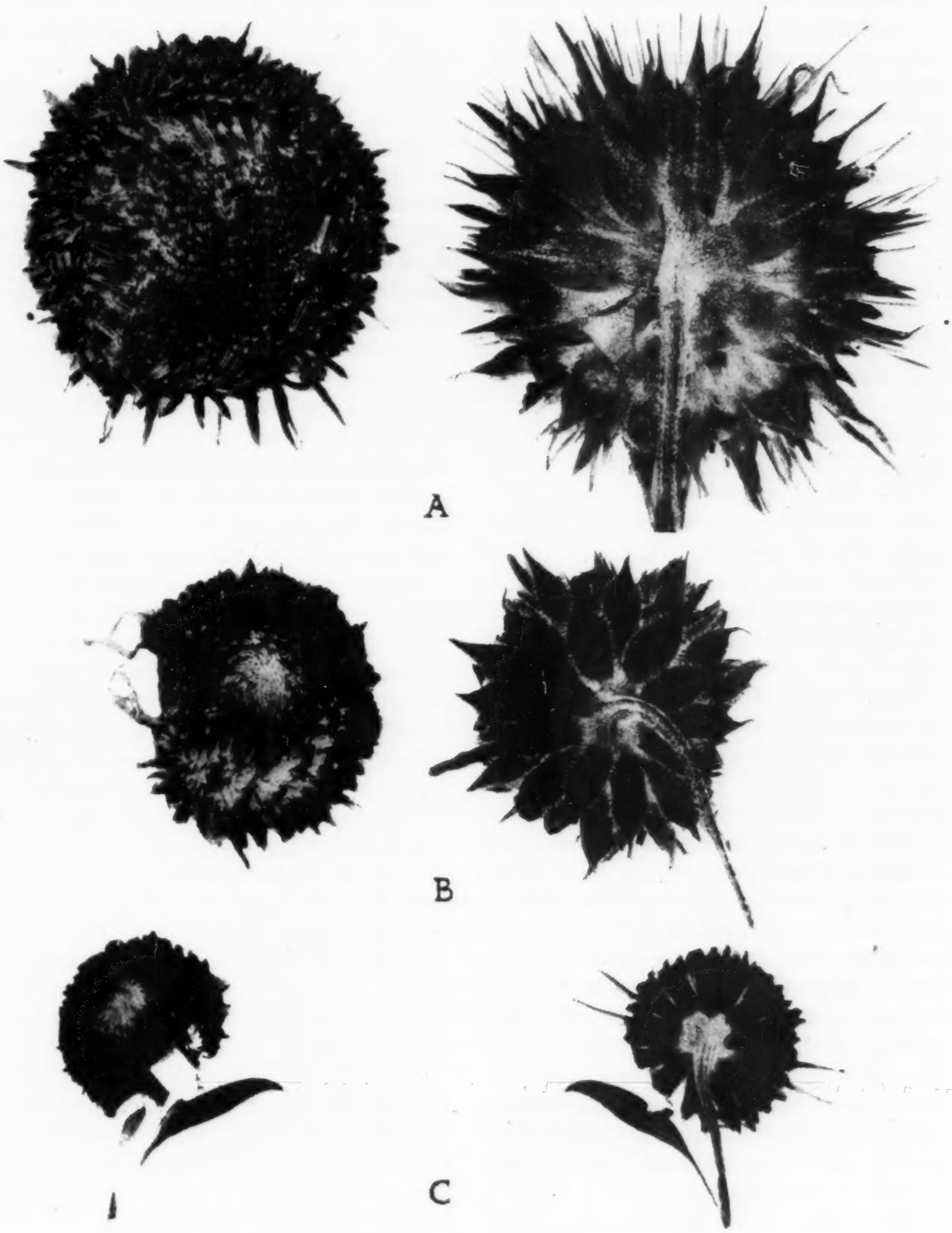

FIG. 5. Heads of *Helianthus annuus*, natural hybrid, and *H. petiolaris*. (A) *H. annuus* from St. Louis, (B) a natural hybrid from East St. Louis hybrid swarm, (C) *H. petiolaris* from St. Louis. On the left, face views showing disk flowers and chaff. On the right, rear views showing the involucral bracts. Rays not shown. Slightly enlarged.

mutation may equally well be responsible for some of these differences, but in view of the fact that the two species do hybridize it would appear that introgression is, at least, partially responsible. The full extent of the introgression is a problem that will require a great deal of additional field work in the West.

Conclusions

The term "introgressive hybridization" was first used by Anderson and Hubricht (1938) to explain the infiltration of the germ plasm of one species of *Tradescantia* into another as the result of hybridization. Since that time further evidence for introgression has been obtained from many plants. Goodwin (1937), Riley (1938, 1939) and Wetmore and Delisle (1939) have made rather detailed studies utilizing experimental methods. A review of the literature on the work dealing with introgression and a discussion of the mechanisms and consequences of introgression will be published elsewhere.

The result of hybridization between *H. annuus* and *H. petiolaris* certainly falls into the category of introgressive hybridization. Although the hybrid is rather highly sterile some good pollen is produced which would allow for backcrossing to the parent species. That such backcrossing of the hybrid occurs is evident from the examination of hybrid swarms.

Dobzhansky (1941) is inclined to be rather skeptical of the great number of hybrids that have been reported. He points out that the putative hybrids may be remnants of the ancestral population from which the two supposed species have differentiated, and further that mutations arising within one species may resemble certain of the characters found in another species. The writer feels, however, that in the present case there can be little doubt that the putative hybrids are actual hybrids. The natural hybrids morphologically agree very closely with the synthetic hybrids. Furthermore, when seeds from a putative hybrid are planted they give rise to diverse types approaching the parent species in appearance. In addition, the high degree of sterility in the putative hybrids indicates that these plants are of hybrid origin.

Of course, as Huskins (1929) has pointed out, what constitutes a hybrid depends upon what one calls a species. It is perhaps well to state here the writer's reasons for considering *H. annuus* and *H. petiolaris* species. Morphologically there are many differences between the two, implying that they differ for numerous genes. The hybrid between the two shows abnormalities at meiosis, indicating that there are chromosomal differences. There are also slight differences in ecological preference and time of blooming; thus the species show reproductive isolation from each other. Although the two are now sympatric they may have at one time been allopatric.

It is possible that the two species may have descended from the same prototype. With the present knowledge of the genus *Helianthus* that can be neither proved nor disproved. Introgressive hybridization is known to take place between *Helianthus annuus* and *H. Bolanderi* (Heiser, 1947), and is suspected to occur between *H. annuus* and *H. cucumerifolius*. It may be found that all of the annual sunflowers are capable of exchanging genes. However, it is the opinion of the writer that all of the annual sunflowers, defined in the narrow sense, have existed as independent species for long periods of time and that hybridization between them may not have occurred before the coming of man.

The two species under consideration here would fall into the category of "ecospecies" following the definition of Clausen, Keck, and Hiesey, and the annual sunflowers as a whole would then belong to a single "cenospecies."

Dobzhansky stated in 1941 that it was impossible to appraise the evolutionary significance of introgressive hybridization at the present time. However, he does suggest three possible roles of introgression. (1) Physiological barriers may develop in response to the challenge of hy-

bridization and therefore introgression may be a passing stage in species formation. (2) Introgression may lead to an obliteration of differences between incipient species and to their fusion into a single highly variable one. (3) If the environment in which the incipient species was formed should cease to exist, some of the recombination products might be more fitted to the new environment than were the parental species; introgressive hybridization might then result in the emergence of superior genotypes.

It is difficult to evaluate fully these possible roles for the case of *H. annuus* and *H. petiolaris*. Although complete physiological barriers to hybridization may appear, none seems to have done so as yet. There is no evidence that introgression is merely a passing stage in the formation of these two species, nor is there any evidence that the hybridization is resulting in the formation of a single highly variable species. Although the introgressants may show characteristics of the other species they can usually be regarded quite definitely as one species or another. Marsden-Jones and Turrill (1929) found that hybridization between *Silene maritima* and *S. vulgaris* had not resulted in their amalgamation into one polymorphic species.

In the case of *Helianthus annuus* and *H. petiolaris* introgression apparently has resulted in the appearance of some superior genotypes among the many recombinations. The spread of both species into new habitats as weeds may have come about through aggressive recombination products. These successful recombination products, representing introgressants, have been able to inhabit new areas. It may prove that many weeds have evolved through a similar process and that they owe much of their aggressiveness and weedy tendencies to introgression.

Although introgression has increased the polymorphy of the two species, it is not the sole cause of the great variability. Gene mutation may have played an important role, and in the case of *H. annuus* hybridization with other annual species and crossing with the cultivated sunflower (Heiser, 1947) have been important factors. Introgression is not the only answer but certainly it should help contribute to the explanation of many problems that have long puzzled taxonomists.

Summary

The sunflower species *Helianthus annuus* and *H. petiolaris* are widespread weeds in North America. Most botanists have held that the two species are indigenous to the Great Plains region. Although the two species are now sympatric in their distribution, they may have been allopatric at one time. There are slight differences in ecological preference and in time of blooming between the two species. Both species possess seventeen pairs of chromosomes. The F_1 shows some abnormalities at meiosis and consequently is rather highly sterile.

Hybrid swarms between the two species have been found in Arizona, Illinois, and Missouri. Two of these hybrid swarms are analyzed on the basis of pollen and seed fertility and the variability of the disk diameter. Comparison of the artificial with the putative natural hybrids tends to verify that the latter are truly of hybrid origin.

In nature it appears that introgression has occurred through backcrossing of the hybrids to their parents. The main consequence of the introgression has been to increase the variability of the two species without any tendency for an amalgamation of the two into a single highly variable species. It is suggested that introgression has been of importance in the development of superior genotypes which may have increased the ability of the two species to spread as weeds.

Literature Cited

Anderson, E. 1936. Hybridization in American Tradescantias. Ann. Mo. Bot. Gard., **23**: 511–525.

—— AND L. HUBRICHT. 1938. Hybridization in *Tradescantia*. The evidence for introgressive hybridization. Am. Jour. Bot., **25**: 396–402.

BLAKE, S. F. 1942. Compositae, in Kearney and Peebles, Flowering plants and ferns of Arizona, U. S. Dept. Agr. misc. publ. 423.

CLAUSEN, J., D. D. KECK, AND W. M. HIESEY. 1939. The concept of species based on experiment. Am. Jour. Bot., **26**: 103–106.

COCKERELL, T. D. A. 1902. De Vriesian species. Nature (London), **66**: 174.

——. 1915. Specific and varietal characters in annual sunflowers. Am. Nat., **49**: 609–622.

——. 1918. A new hybrid sunflower. Torreya, **18**: 11–14.

DEAM, C. C. 1940. Flora of Indiana. Dept. of Conservation. Indianapolis, Ind.

DOBZHANSKY, TH. 1941. Genetics and the origin of species. Revised Edition. Columbia University Press.

GEISLER, F. 1931. Chromosome numbers in certain species of *Helianthus*. Butler Univ. Bot. Studies, **11**: 53–62.

GOODWIN, R. H. 1937. The cytogenetics of two species of *Solidago* and its bearing on their polymorphy in nature. Am. Jour. Bot., **24**: 425–432.

HEISER, C. B. 1947. Variability and hybridization in the sunflower species *Helianthus annuus* and *H. Bolanderi* in California. Ph.D. Thesis (Unpub.), Univ. of Calif. Library, Berkeley.

HUSKINS, C. L. 1929. Criteria of hybridity. Science (n. s.), **69**: 399–400.

MARSDEN-JONES, E. M., AND W. B. TURRILL. 1929. Researches on *Silene maritima* and *S. vulgaris* II. Kew Bull. of Misc. Information, **2**: 33–38.

PUTT, E. D. 1941. Investigations of breeding technique for the sunflower (*Helianthus annuus* L.). Scientific Agriculture, **21**: 689–702.

RILEY, H. P. 1938. A character analysis of colonies of *Iris fulva, I. hexagona* var. *giganticaerulea* and natural hybrids. Am. Jour. Bot., **25**: 727–738.

——. 1939. Introgressive hybridization in a natural population of *Tradescantia*. Genetics, **24**: 753–769.

WATSON, E. E. 1929. Contributions to a monograph of the genus *Helianthus*. Papers Mich. Acad. of Science, Arts, and Letters, **9**: 305–475.

WETMORE, R. H., AND A. L. DELISLE. 1939. Studies in the genetics and cytology of two species in the genus *Aster* and their polymorphy in nature. Am. Jour. Bot., **26**: 1–12.

ANNOUNCEMENT

The 13th International Congress of Zoology will take place in Paris in 1948 from Wednesday, July 21, to Tuesday, July 27. It will include a section "Evolution and Genetics."

The Executive Committee of the Congress proposes the following three subjects for special discussion in this section:

1. The differentiation of geographical races and the role of ecological factors in speciation.
2. Physiological and biochemical races in systematics.
3. Natural selection.

Each of these questions will be made the subject of a discussion based on one or several original or review papers.

All biologists who are interested in these problems and wish to participate in these discussions are requested to get in touch with the President of the section, M. Georges Teissier, Laboratoire de Zoologie de la Sorbonne, 1 Rue Victor Cousin, Paris.

All other inquiries concerning the Congress should be addressed to the General Secretary, M. Fisher-Piette, Professeur au Muséum, 55, Rue de Buffon, Paris V, France.

ECOLOGICAL FACTORS IN SPECIATION

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The past decades have seen the gradual formulation of the theory of geographical speciation, principally based on work in the fields of the systematics of mammals, birds, insects, and mollusks. This theory postulates that in bisexual animals a new species can develop only "if a population, which has become geographically isolated from its parental species, acquires during this period of isolation characters which promote or guarantee reproductive isolation when the external barriers break down" (Mayr, 1942). A number of workers in recent years have considered this statement an oversimplification. The omission of any reference in this description of the speciation process to the ecological factors—so vitally involved in the process of speciation—has also been objected to. Even though the importance of geographical speciation is universally admitted, there are a number of authors, particularly among the ichthyologists and entomologists, who believe that in addition to geographical speciation there is another process of speciation, variously referred to as ecological or sympatric speciation. Thorpe (1945), for example, is inclined to consider that in addition to geographical speciation there is a speciation process which is characterized by the fact "that local differences of habit may be the starting point for the evolution of new species."

It appears to me that there is no real conflict between those authors who stress the ecological aspects of speciation, such as Stresemann (1943) and Thorpe (1945), and those who, like myself, have stressed the geographical aspects. This was pointed out by Timofeeff-Ressovsky (1943). The seeming differences are due partly to misunderstandings and partly to a different emphasis placed on various aspects of a single process of speciation. The field has suffered from looseness of thought and vagueness of expression, and it may therefore be useful to attempt a fresh analysis and possibly a synthesis of the two viewpoints. The principal obstacle blocking such synthesis up to now has been that those authors who have emphasized the role of ecological factors in speciation generally accept sympatric speciation as an integral part of ecological speciation. To remove this difficulty, a special section (pp. 269–285) has been devoted to a discussion of sympatric speciation. It is more important, however, to determine the respective roles of geographical and ecological factors in speciation, and to find out whether they operate consecutively or concomitantly.

The field has suffered particularly from the lack of a clear-cut *Fragestellung*. The result has been that only few investigations have ever been undertaken which would give decisive answers to the unsolved questions. Most of the published studies sadly miss the crucial points. It is one additional object of this discussion to focus the attention of investigators on those aspects that are in particular need of further study.

I. THE PROCESS OF SPECIATION AND THE ROLE OF ECOLOGICAL FACTORS

The most important aspect of speciation is that it is a process involving populations rather than individuals—contrary to the views of De Vries and other early Mendelians. The gene pool of a whole

population serves as "the material basis of evolution," which is so often referred to in the genetic literature. The problem of speciation then boils down to two questions:

(1) *How do new populations* [1] *within a species develop?*
(2) *How do such populations become reproductively isolated from other populations of the parental species?*

Two steps are thus involved in speciation, (1) the establishment of new populations and (2) the establishment of intrinsic reproductive isolation. Geographic speciation assumes that, as stated, the sequence of these steps is 1–2. Sympatric speciation assumes that the first step is the origin of reproductively isolated individuals which subsequently establish a new species population. This is a logically consistent hypothesis since two separate sympatric populations cannot exist unless they are reproductively isolated. The objections to this sympatric speciation hypothesis will be fully stated in the second section. But, first an attempt shall be made to answer the following questions: How does the theory of geographic speciation explain the origin of new populations and of reproductive isolation between them? How does it evaluate the role of ecological factors in these processes? Furthermore, what is understood when the expression "geographically isolated" is used?

What is Geographical Isolation?

When two populations are separated by such a formidable barrier as a vast desert, or an ocean, or an extensive, high mountain range, everyone will agree that they are geographically isolated. However, is a corn field geographically isolated from the next corn field by an intervening wheat field? How large must the distance be between "isolated" populations? How much gene flow is permissible?

Unfortunately, no general answer can be given to these questions. It depends on the circumstances of each case. The less suitable a given habitat is for a species, the more efficient a barrier it becomes. The term "geographically isolated" is to be construed broadly and refers to any environmental factor that effectively inhibits gene flow between two neighboring populations. In addition to the macrogeographical isolation of the above listed geographical barriers, there are many cases of *microgeographical isolation* where no great distances nor conspicuous barriers are involved. The terms topographical or spatial isolation have often been used for these situations, particularly in the case of species with short average cruising range, such as are typical for many invertebrates. However, opposing the terms geographical and spatial isolation creates the erroneous impression that two different principles are involved. This is not the case. Whether large or small distances are involved, in all these instances there is a stretch of unsuitable terrain which inhibits dispersal and thus reduces gene flow. The term "microgeographical isolation" is thus preferable to "spatial" or "topographical" isolation.

All the terminologies so far proposed break down in those cases where two populations that differ in their ecological requirements are in contact but do not overlap. Are they species or subspecies? Should they be called sympatric or allopatric? In the narrowest sense, they are, of course, allopatric but, carrying the argument to the limit of absurdity, are not any two individuals allopatric? The terms sympatric and allopatric have been very useful in focussing attention on the spatial relationship of natural populations, but they seem to become meaningless in those cases where ecologically different populations exclude each other in space.

[1] A population is a group of freely interbreeding individuals of a locality. Separate sympatric populations belong, by definition, to different species. Separate conspecific populations must, also by definition, be allopatric during their breeding season (except in the rare cases of seasonal separation in zones of secondary overlap).

If a meadow and a forest species occur in the same general region, are they allopatric or sympatric? This problem is particularly acute where habitats occur as widespread features of the landscape, sharply delimited against each other, such as is frequently found in the tropics and subtropics or wherever the original landscape has not yet been disturbed too severely by man. Here, differences in ecology are also such of geography. The reality of this problem is evident to every naturalist.

In a recent letter Mr. R. E. Moreau wrote me about the following situations concerning African birds. "In each of the mountains of East Africa a mountain forest white-eye (*Zosterops*) is found which is isolated as completely from the other montane ones as if it inhabited an oceanic island. I doubt whether any one of them comes into regular contact with the non-forest species (*Z. senegalensis*) which entirely surrounds them geographically but seems to avoid the immediate neighborhood of forest patches. An even more critical example of this sort of thing is provided by the two drongos, *Dicrurus ludwigii* and *D. adsimilis*. The former, in my experience, never ventures outside the edge of the evergreen forest, the latter seems never to perch even on the outside edge of a forest tree. Yet, both may occur within 50 yards of each other and the latter species is quick to occupy a clearing made in evergreen forest. I have come across some other nice examples, such as where *Cossypha heuglini* and *C. semirufa* occur in the same locality. The former is always restricted to its normal habitat, namely, bush country outside the forest, while the latter is found only in the forest. In one or two mountain forests where *C. semirufa* is absent the other bird replaces it. Are these species sympatric or allopatric?"

A universally applicable answer cannot be given to all the above questions. They must be answered from case to case and the answer inevitably will depend on the circumstances.

The Invasion of New Habitats

The process of speciation results in ecological diversification and consequently in an ever-increasing efficiency in the utilization of the environment (Mayr, 1948b; Lack, 1948). One aspect of gradual speciation is therefore that it is an ecological process. Every species lives on an adaptive peak and the problem of speciation is how to reach new, not previously occupied, adaptive peaks. A species might do this either (1) by becoming locally more euryoecous (ecologically tolerant) or (2) by invading new areas with different ecological conditions. As far as the first possibility is concerned, a population that was previously restricted to the forest might become adapted to live in orchards or meadows as well as in the forest. Observations show that this occurs only very rarely. A species that is adapted for life in the forest will normally not be able to survive the competition it meets in the meadow. A population adapted to live on one species of food plant will normally not be able to enlarge its niche to include a second kind of food plant, unless its genetic make-up is altered. To be sure, individuals of many species try continuously to invade new niches. Such colonizations are often temporarily successful, but a single adverse season usually reduces the ecological amplitude of the species to its normal width. Some species are, at least locally, restricted to an extremely narrow niche, others are more tolerant in their ecological requirements. Whether its niche will be broad or narrow is largely a function of the genetic constitution of the respective population. A local gene complex can become modified by the usual genetic processes so as to increase or decrease the ecological tolerance of the population of which it is the genetic basis, but the development and simultaneous maintenance in the same area of two different gene complexes adapted for two different ecological niches will be prevented by gene flow. Some especially successful

species, the euryoecous species of the ecologist, get around this difficulty by developing a gene complex that is equally satisfactory in a number of different habitats. Such species are, however, rather rare.

How then does a species colonize a new type of habitat? A glance at the distribution map of ecologically variable species gives us a clue. The ecologically (as well as genetically) most aberrant populations are nearly always found along the periphery of the range of the species. This has several separate reasons. One of them is that the one-directional gene flow near the border of the range increases the rate of evolutionary change, another is that the normal habitat in the center of the range may not offer optimal living conditions near the periphery, a situation that encourages a shift in habitat. Many specialized species have been able to develop in each district a geographical race adapted for the locally most abundant or otherwise most satisfactory ecological niche. The Red Crossbill (*Loxia curvirostra*) offers a particularly graphic illustration of this important principle (Kirikov, 1940). The mountains of central Asia (Himalayas, Altai) were probably the original home of the species. It lives there on the prevailing coniferous trees, various species of spruce (*Picea*) or larch (*Larix*), and has developed a rather thin, slender bill. From here the crossbill has spread east and west and has reached a number of areas where pines (*Pinus* spec.) are the prevailing or exclusive tree, such as in the Crimea (*L. c. mariae*), in Tunisia (*L. c. polyogyna*), in the Balearic Islands (*L. c. balearica*), and particularly in northern Europe (*L. c. pityopsittacus*), also in the southwestern United States and Central America. In these areas geographical races of the crossbill have developed which have large, heavy bills adapted to the opening of the tough pine cones. However, only one race has developed in the areas where there are two prevalent conifers, such as *Pinus cembra* and *Picea excelsa* in the Alps. The Crossbill of the Alps (*L. c. curvirostra*) is a spruce race. The only apparent exception occurs in parts of northern Europe where the "subspecies" *curvirostra* and *pityopsittacus* are reported to breed in certain districts side by side without mixing. The greater portion of the ranges of these two forms is, of course, still separate, revealing their geographical origin. The evidence indicates that the most distinct of these "ecological" races originated in complete geographical isolation. This is, of course, even more true for the "ecological" races among the Galapagos Finches (Lack, 1947) and Hawaiian Honeycreepers (Amadon, 1947).

At first sight the concept of a geographically and ecologically variable species seems full of contradictions. We see that in one locality a species is restricted to a very definite habitat niche, while in another locality it occurs in a different, sometimes very different, niche. We know that through selection in each of these populations a definite gene complex has developed, which permits the population to survive and thrive in spite of competition, predation, and all sorts of other adversities. I had asserted in 1942 (p. 196) that geographical isolation precedes the formation of ecological preferences in every case. If this were true how could species ever invade new habitats, as they undoubtedly do? Thorpe (1945) correctly points out this contradiction.

There is thus great need for studies by experiment and observation under what conditions individuals of a species can shift to new habitats and become the progenitors of new populations. Unfortunately, the evidence is scanty and has been interpreted in various ways. It is this aspect of the speciation problem that has been given special attention by Thorpe.

The adaptation for life in a given habitat includes the faculty of the individual of the species to select this habitat (from a vast array of other possible ones!) during the dispersal phase. Although genetic

factors must to some extent control this ability of habitat selection, nevertheless it is not entirely rigid and undeviating. There is a certain amount of ecological plasticity which is greater in some species, less in others.

The establishment of individuals in a new environment will be assisted by conditioning, as emphasized by Thorpe (1945), as well as by "organic selection," that is, the gradual substitution of modifications by mutations (Baldwin, 1902; Gause, 1947). A new population within the species will thus come into being and will permit the species to spread into areas that were previously outside the breeding range. It is probable that most range expansions of species are caused by the origin of such new intraspecific populations. This is well illustrated by the recent spread of the Mistle Thrush (*Turdus viscivorus*) in northwestern Europe (Peitzmeier, 1942). This species had lived for a long time in the coniferous mountains south of Westphalia, but did not invade the lowlands until 1928. By 1939 it was common in the deciduous woods and farm gardens of the area, a habitat strikingly different from the pine and spruce forest of the nearby mountains. Peitzmeier, in tracing this invasion back to its source, presents evidence which shows that it did not come from the neighboring mountains but rather from the west (northern France, Belgium) where the Mistle Thrush had always been an inhabitant of deciduous lowland woods and gardens. From here it spread eastward through Holland and across the Rhine into Westphalia. Thus the invasion of the deciduous woods of Westphalia is not due to a shift in the tolerance of the population from the coniferous woods of the hills around Westphalia, but due to the range expansion of an already existing deciduous woods population. Unfortunately, nothing is known as to the relationship of the two populations, but it is quite possible that at the present time there is very little gene exchange between these two geographical-ecological races of the Mistle Thrush. It would be interesting to determine through banding whether there is any interbreeding in the zone of contact. It would also seem important to determine where and how the deciduous woods population of northern France had originated.

Not always are the ecological differences as clearly associated with geographical features (different distributions) as in the case of the Mistle Thrush. The smaller the normal cruising range of individuals of a species, the smaller becomes the geographical range of a local population, and the more difficult it is to discern that the establishment of new populations is a microgeographical phenomenon rather than a purely ecological one. The literature of economic entomology is replete with cases of locally segregated populations showing ecological differences. The Codling Moth (*Carpocapsa pomonella*) is particularly apt to develop such local races. Armstrong (1946) recently described a local population of this species from the Province of Ontario (Canada) which had developed in a large, eighty-year old pear orchard, which "is more or less isolated from other large pear or apple orchards." While moths in Ontario apple orchards have their peak of emergence between June 26 and July 17, the moths in this pear orchard emerged mainly between July 17 and August 7, thus two weeks later. The delayed emergence of the pear moths coincided with the period during which the pears softened and became penetrable for the larvae. Armstrong points out that only "the absence of large apple orchards in the vicinity has prevented this strain from being swamped by crossing with the generally prevailing apple strain." For, even though the peaks and extremes of the emergence curves are well separated, there is still a large area of overlap of emergence time which would result in rapid swamping if it was not for the geographical segregation.

Several other populations of the apple codling moth are known that have in-

vaded other hosts and have developed partly microgeographically-segregated and biologically-distinct populations. In California and in other areas the codling moth attacks the walnut. The first damage to walnut crops in California was reported in 1909. The first heavy infestation was in 1931 although apples and pears had been heavily infested in nearby districts since 1880 (Boyce, 1935).

This interesting case has never been analyzed fully. It is not known whether there are two separate strains of the codling moth in the walnut districts or whether the ecological requirements of the local race have become broader, permitting life both on apple and walnut. There is comparatively little apple growing in the chief walnut districts, and it appears possible that the codling moth population in the walnut districts has changed completely into a "walnut strain." It would be intensely interesting to follow up these possibilities. All we know up to now is that an evolutionary change has occurred in the apple codling moth of the walnut-growing districts of California, since it has invaded a new host fifty years after its introduction into California. The existence of such cases is not necessarily proof for sympatric speciation since, as stated, there are several alternative possibilities.

Amount of Gene Flow Between Incipient Species

All geographical barriers are relative. Even the most isolated islands are frequently visited by strays from the nearest mainland. Hundreds of continental species of animals are annually recorded from Great Britain. The interruption of gene flow even between two "isolated" populations is thus always relative and incomplete (figure 1B). If two such populations diverge nevertheless, it proves that the combined effects of mutation pressure, selection, and random fixation (+ recombination) outweigh the equalizing effects of gene flow.

This leads to the simple, but important, question: How strong must the gene flow be to prevent the genetic drifting apart of two populations? It is very unlikely that the purely genetic processes of mutation pressure and random fixation cause changes of a sufficiently high order of magnitude to hold any sizable gene flow in check. It may be different with selection pressure, but unfortunately it has never been determined how much gene flow strong selection pressure can neutralize.

Let us consider, for example, two spatially segregated, contiguous populations within a species which are not separated by an extrinsic barrier. Selection pressure will tend to pull these two populations apart, if they live in rather different habitats. But, can selection overcome the effects of dispersal across the zone of contact? Can conditioning reduce dispersal across the line of contact to such an extent that it no longer prevents the steady divergence of this population? Sufficient facts are not available for a decisive answer to these questions. The scanty evidence that is available indicates that speciation by geographical segregation (without isolation) is rare, if it occurs at all. Ecological differences are rarely abrupt in zones of primary intergradation. There is likely to be an intermediate habitat with an intermediate population to serve as a channel for the gene flow. In the cases where two ecologically very different subspecies are found in immediate contact, it can nearly always be shown that secondary contact is involved.

The only study known to me of the effect of gene flow across a habitat border is an investigation by Blair (1947) of the deermouse (*Peromyscus maniculatus*) populations on pinkish gray and dark red soils in the Tularosa Basin. Populations that occur eighteen miles apart on differently colored soils show adaptive differentiation in the frequency of buff and gray genes. However, there was no difference between the populations found in two stations on different soils only four miles apart. Future investigations must

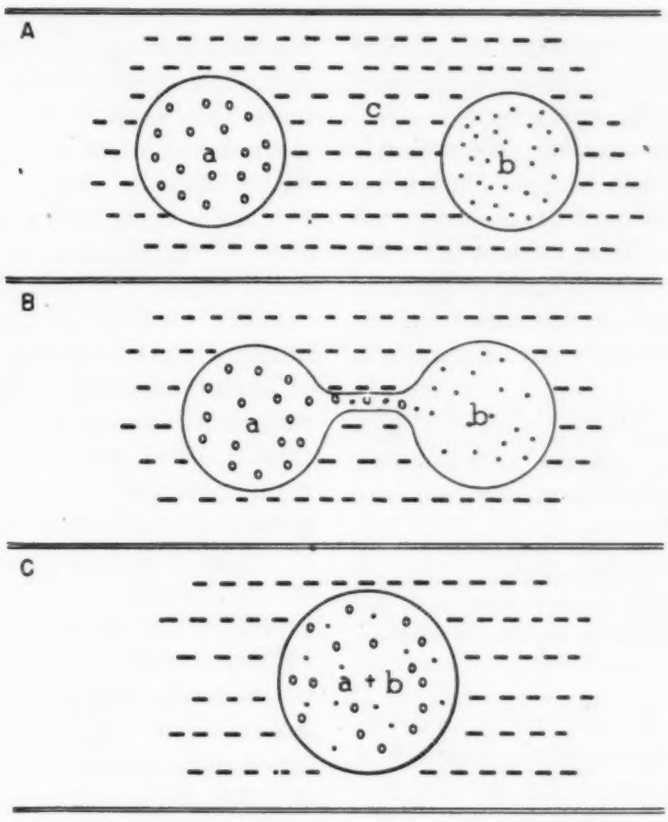

FIG. 1. Spatial relationship of two populations a and b (diagrammatic). A. Completely isolated by unsuitable terrain. B. Incompletely isolated; some gene exchange through partial barrier. C. Completely sympatric, but partially or completely segregated in different ecological niches.

show to what extent a stronger habitat preference can reduce the width of the dispersal belt.

It is unfortunate that so little evidence is available on this problem. Sympatric speciation would appear more probable if speciation by geographic segregation was at all common. It is here that the chief difference of opinion seems to exist between those who believe in occasional sympatric speciation and those who do not. The adherents of sympatric speciation believe that invasions of new—geographically not isolated—habitats are sufficiently irreversible and conditioning for these new habitats sufficiently complete to prevent dispersal and permit the building up of distinct gene complexes. A thorough examination of the whole problem of sympatric speciation is therefore essential for the proper evaluation of the various possibilities.

II. AN ANALYSIS OF SYMPATRIC SPECIATION

The role of ecological factors in geographic speciation was discussed in the preceding section. The present section shall be devoted to answering the question whether or not there is a separate process of sympatric speciation, independent of geographic speciation. What "sympatric speciation" is has never been properly defined, but it is generally characterized by one or both of the following assumptions: (a) the establishment of new populations in different ecological niches within the normal cruising range of the individuals of the parental population (figure 1C), (b) the reproductive isolation of the founders of the new population from individuals of the parental population. Gene flow between daughter and parental populations is inhibited by in-

trinsic rather than extrinsic factors. A rapid, if not almost instantaneous, process of species formation is implied in most schemes of sympatric speciation.

Historical. The concept of sympatric speciation goes back to pre-Darwinian days. Darwin himself was uncertain about this question as is evident from his correspondence with Wagner, Semper, and Weismann, and as indicated in numerous passages in his works, e.g.:

> "If a variety were to flourish so as to exceed in numbers the parent species, it would then rank as the species, and the species as the variety; or both might co-exist, and both rank as independent species."
>
> "The small differences distinguishing varieties of the same species, steadily tend to increase till they come to equal the greater differences between species of the same genus, or even of distinct genera."

Darwin makes no distinction between speciation through individuals (individual varieties) and speciation through populations (subspecies). While in some of his statements he seems to place due weight on the geographical element, in others he seems to ignore it altogether. It was M. Wagner who, in a series of papers from 1868 to 1889, brought out the importance of geographical isolation of populations for the multiplication of species. At first these ideas found few adherents, radical and novel as they were. On the contrary, the last two decades of the nineteenth century witnessed the greatest flowering of the concept of sympatric speciation. Romanes devoted an entire volume of his book *Darwin and after Darwin* (1897) to a theory of sympatric speciation which he called the theory of physiological selection. He and his followers insisted that geographical speciation was only of minor importance for the origin of new species. The argument of this school is based on two concepts, one unproven and very unlikely (that of homogamy), and the other definitely wrong (that of blending inheritance). Since they took blending inheritance for granted, they had to postulate the existence of homogamy (see also Pearson, 1900). The concept of homogamy or associative mating states that within a population the most similar individuals will mate with each other. For "so long as there is free intercrossing, heredity cancels variability, and makes in favour of fixity of type. Only when assisted by some form of discriminate isolation [= preferential mating], which determines the exclusive breeding of like with like, can heredity make in favour of change of type, or lead to what we understand by organic evolution" (Romanes). The most significant point of this argument is that new populations are formed by the non-random mating of individuals within populations. Romanes' theory is merely an elaboration of the theories first independently proposed by Catchpool (1884) and by Dahl (1889). All these theories have three postulates in common (which shall be discussed below): homogamy, complete linkage of mate selection and habitat selection, and the absence of genetic segregation.

The confused reasoning of this school cannot be illustrated better than by the following quotation:

"Suppose that on the same oceanic island the original colony has begun to segregate into secondary groups under the influence of natural selection, sexual selection, physiological selection, or any of the other forms of isolation, there will be as many lines of divergent evolution going on at the same time (and here on the same area) as there are forms of isolation affecting the oceanic colony" (Romanes, 1897). Actually, of course, exactly the opposite is true. Isolated oceanic islands are exemplary for monotypic evolution as Lack (1947) has demonstrated so convincingly in connection with the Cocos Island Finch.

It would be foolish to quote these fallacies if it were not for the fact that the very same arguments are still used today to endorse sympatric speciation. The only novel feature is that nowadays the occurrence of "macromutations" is sometimes postulated, as for example by Valentine (1945): "Speciation may proceed

within a population as a result of the appearance of relatively drastic changes (mutations) that are recognized by both the mutants and the norms, causing reluctance to cross. This, in brief, is the principle of associative speciation."

The Evidence for Sympatric Speciation

There must be some reasons why there are still so many authors left who believe that a process of sympatric speciation occurs in addition to allopatric (geographical) speciation. Botanists, in particular, have frequently stated that they find relatively little evidence for geographical speciation. Romanes (1897) quotes Nägeli to the effect "that in the vegetable kingdom closely allied species are most frequently found in intimate association with one another, not, that is to say, in any way isolated by means of physical barriers." In fact, *all* of the cases quoted by Romanes as proving sympatric speciation are taken from the plant kingdom. As is now known, instantaneous sympatric speciation through polyploidy is actually a common occurrence among plants. Apomixis, hybrid swarms, and the polytopic formation of ecotypes further complicate the picture. On the other hand, speciation in sexually reproducing plants seems not to differ materially from speciation among sexually reproducing animals.

Two classes of phenomena are frequently quoted as proving the existence of sympatric speciation. One consists of experiments showing that parasitic insects, as well as monophagous or oligophagous food specialists among plant feeders, can be conditioned to accept new hosts. The other is the occurrence of "species swarms" among freshwater organisms in many reputedly rather recent lakes where, it is believed, geographic speciation could not have been operating. The significance of this evidence shall be discussed below.

The main reason for postulating sympatric speciation, however, seems to be the fact that invariably there are ecological differences between closely related and morphologically similar sympatric species. This ecological specialization leads to a wonderfully efficient way in which the numerous species of a locality utilize their environment. It is argued that such perfect adaptation could not have developed in geographical segregation. There is a strong reluctance among naturalists against admitting the evolutionary role of accident. Just as the Lamarckian finds it impossible to believe that the wonderful morphological adaptations found in nature could be the result of random mutation and selection, in a parallel manner some ecologists find it hard to accept that ecological speciation should happen in the apparently round-about way of spatial segregation rather than by the direct route of sympatric habitat choice.

Assumptions Underlying the Concept of Sympatric Speciation

The thesis of sympatric speciation cannot be discussed profitably before some of the assumptions are stated more succinctly that are made by the adherents of this thesis. Two recent papers contain a clear statement of the major assumptions. Thorpe (1945) visualizes the following procedure of sympatric speciation:

> "Imagine now an area where two types of habitat 'a' and 'b' (e.g. two different vegetational types) are available in mosaic distribution and a species (of bird) confined to habitat 'a' within that area. In some exceptional circumstances of crisis or as a result of some slight germinal change certain individuals of the species spread into habitat 'b' and the young reared there become imprinted, or otherwise specialized, to the new niche. If this niche provides room for expansion, the birds of the new habitat will rapidly come to fill it during which time they will be reproductively isolated to a considerable extent from the 'a' habitat birds."

In this scheme Thorpe implies thus the assumptions (1) that young birds raised in a new habitat will "become imprinted, or otherwise specialized, to the new niche" to such a degree that they will not reenter the ancestral habitat to any appreciable extent, but rather establish at once a new

population by a more or less irreversible process. (2) That such individuals "will be reproductively isolated to a considerable extent" from the inhabitants of the ancestral habitat by being completely restricted to the new habitat. The choice of habitat and not microgeographical segregation would be the isolating factor since the two habitats are "available in mosaic distribution" (see figure 1C).

Test (1946) considers sympatric speciation as a preadaptation process. "Ecological speciation is that differentiation which has taken place during isolation of extreme variants which could not survive in the parental microhabitat, but which are able to take over a microhabitat not compatible with the parental morphology and ecology. This isolation is not of a geographic type, but is due to the unsuitability for the parent stock of the microhabitat invaded by the offshoot." In connection with this hypothesis the following assumptions are made explicitly or by implication:

(1) That new species may be established by extreme individuals rather than by populations.

(2) That such founders and their offspring are different genetically from the parent population.

(3) That such founders are preadapted for a habitat different from the parental habitat.

(4) That—in order to survive—such individuals search for the habitat for which they are preadapted.

(5) That during the original colonization "an intervening area" can be crossed which later no longer can "be crossed by individuals of either stock."

Each of these assumptions is arbitrary and largely unsupported by facts. Combining several of these improbable assumptions into a single hypothesis increases their improbability.

Objections to the Hypothesis of Sympatric Speciation

Every one of the various proposed hypothetical models of sympatric speciation makes certain unproven assumptions. Obviously, even if all these assumptions should turn out to be invalid, it would not necessarily prove that the basic hypothesis is wrong. In any case, a critical evaluation of the various assumptions will lead to a clearer understanding of the problem.

(*a*) *Homogamy.* The concept of homogamy states that within a population the most similar individuals will prefer to mate with each other. The postulation of homogamy was the inevitable consequence of the theory of blending inheritance because random mating would soon lead to a complete elimination of genetic variability in a population under the theory of blending inheritance. Dahl (1889), Romanes (1897), Pearson (1900), and many other writers of that period who were unaware of the prevalence of geographical speciation, claimed that homogamy was an indispensable requisite of speciation. However, positive evidence for the occurrence of non-random mating within populations is exceedingly meager. Exceptions are provided by species that are very variable in size and continue to grow after reaching maturity. In the nudibranch *Chromadoris zebra*, for example, Crozier (1918) found that courtship usually broke off between individuals of too uneven size and that there was considerable correlation (about 0.6) between the sizes of the sexes in copulating pairs. However, in this and other similar cases there was complete overlapping between neighboring size classes and no evidence for the origin of any discontinuities owing to this associative mating. Furthermore, in many other less variable species (Alpatov, 1925; Spett, 1929) there was no correlation in size between copulating individuals. As far as color characters or other species characters are concerned, the evidence is even more completely negative. Among the numerous cases of polymorphic vertebrates that have been investigated the only known case of probable non-random mating is that of the Snow Goose-Blue Goose (Manning,

1942). Of the 1500 Blue Geese that were nesting on Southampton Island among about 30,000 Snow Geese, 850 formed pure Blue pairs instead of about 180 as would be expected on the basis of random pairing. Unfortunately, these raw data are inconclusive since the distribution in subcolonies was not investigated, and the geese are well known to form small clans. Nor were the heterozygotes taken into consideration in these calculations. Kosswig (1947) suggested recently that homogamy might explain the rapid speciation of cichlid fishes in the East African lakes. Not only does he produce no evidence to support this speculation, but he is definitely in error when he believes that monogamy will necessarily result in homogamy. Gershenson (1941) has been able to prove conclusively that there is random mating among the color phases of the hamster (*Cricetus cricetus*). The same has been shown for color patterns in insects (Spett, 1929). The only apparent exception is the yellow mutant in *Drosophila melanogaster* and probably in other species of the genus (Spett, 1931; Diederich, 1941). However, in this case there is only partial one-directional mating preference and the viability of individuals of this mutant is so inferior to wild type that it would be rapidly eliminated in wild populations. Even where there is a slight amount of homogamy, its role in speciation can apparently be neglected, for Hogben (1946) states (p. 163) on the basis of extensive calculations: "Positive assortative mating can have very little importance as an evolutionary process unless it is exceedingly intense." This discussion can then be summarized in the statement that evidence in favor of homogamy is virtually nonexistent and that homogamy, where it exists, is not of the type that would lead to the establishment of discontinuities within populations.

(*b*) *Linkage of mate preference and habitat preference.* Romanes and others seem to take it for granted that if a species is found at a given locality in several niches, mating occurs only between those individuals that live in the same ecological niche. The choice of a new niche would then automatically result in the establishment of reproductive isolation. The known facts do not support this contention. Copulation in most butterflies and moths, for example, takes place during the dispersal phase of the life cycle (on flowers, etc.) and not on the host plant. If it does take place on or near the host plant, it is usually only the female that is sedentary while the male undertakes relatively extensive flights.

Ecological factors function simultaneously as isolating mechanisms only under two sets of circumstances. First if there is a difference in the breeding period. If one of two closely related species breeds only in sunlight, the other only in darkness, they will be effectively isolated, or, if one breeds only in the spring, the other only in the fall. However, there is always a twilight and a summer to connect the separated breeding periods. Furthermore, there is no evidence or probability that such drastic differences can develop within a single local population nor by single mutations (see below).

The other possibility is furnished by species in which mating always takes place on the host species and host selection is entirely rigid. Such rigid host selection has primarily a genetic basis although it may be reenforced by conditioning. Switching over to a new host would thus be tantamount to the establishment of a new species. The difficulties in this case are several. First of all, there are the heterozygotes that serve as intermediaries between the old and the new host (see below). Secondly, species that are *that* rigidly adapted to one host probably have rather low survival value on a new host, unless the new host is in a different environment. In that case, the scheme would be merely a modification of spatial speciation. However, the mechanism is possible and deserves further investigation. An evolutionary analysis of mo-

nophagous families of insects is badly needed.

(*c*) *Conditioning without isolation.* Thorpe, Cushing, and other recent authors believe that conditioning could under certain circumstances play a considerable role in the origin of new species. This interest in conditioning goes back to a revival of Baldwin's theory of Organic Selection which is most fully stated in his book (1902). This theory states in short that if a population enters a new environment there will be a selective premium on mutations that would give a genetic basis to the previously non-genetic adaptive characters. This process of the substitution of modifications by mutations, which simulates direct action of the environment, has found considerable attention in Russia, as reported by Gause (1947). As a matter of fact, there is nothing strikingly new in this theory. It merely paraphrases two well-known facts, namely that adaptive characters are favored by natural selection, and that the more adaptable a species is the more easily it may enter a new environment. Both of these facts are in harmony with the concept of geographical speciation. To prove that organic selection and conditioning play an important role in speciation, it must be demonstrated that these processes reduce gene flow between the new and the parental habitat below the point where it interferes with the establishment of genetically controlled isolating mechanisms. Do the experiments on conditioning support this assumption?

An experiment by Cushing (1941) conducted in support of the hypothesis that olfactory conditioning is "one way in which an isolation may arise within insect populations" may be analyzed in more detail. A stock of the species, *Drosophila guttifera,* which normally inhabits fungus but had been kept in the laboratory on the ordinary corn-molasses-agar medium, was subdivided into two strains, one continued on this laboratory medium ("controls"), the other on a mushroom extract medium ("mushroom conditioned"). Given a choice of a laboratory and mushroom medium for egg laying, the control flies in four sets of trials (A–D) laid 19.5 per cent eggs on the laboratory medium, while the mushroom conditioned flies laid only 8 per cent of their eggs on this medium. Does this experiment indicate that conditioning can split one population into two? I believe not. To begin with, 80.5 per cent of the eggs laid by flies conditioned and selected for many generations to lay on the laboratory medium chose the mushroom extract medium. This illustrates strikingly the powerful influence of the genetic constitution of these fungus flies. On the other hand, among the reconditioned flies 8 per cent still laid eggs on the laboratory medium. Translating this into terms of the natural environment it means that there would be a continuous very active gene flow from the population in one food niche to the population in the other. Furthermore, contrary to Cushing's opinion, selection seems to have played a role in his and other similar experiments. Even inbred laboratory strains have much concealed variability and the first generation or early generation, in such "conditioning" experiments are often characterized by high mortality. This happened also in the experiment of Meyer and Meyer (1946) who succeeded in transferring a strain of *Chrysopa vulgaris* to a new prey (the coccid *Pseudococcus comstocki*). The success of the experiment is ascribed by the authors to natural selection by means of the survival of those larvae which were physiologically adapted to the new kind of food. There was high mortality in the first three generations. That the selection of the medium on which eggs are deposited has a genetic basis is confirmed also by the work of Masing (1946) who developed lines in a dumpy stock of *Drosophila melanogaster* in which the females preferred either a sugary or a non-sugary medium for egg deposition. The obvious correlation with the intestinal yeast flora was not examined. It may be mentioned incidentally that the attempt by Dobzhansky and Mayr

(1945) to affect the degree of sexual isolation between two species of *Drosophila* by raising the larvae jointly in the same containers was not successful. In conditioning experiments by Thorpe (1939) the possible effect of selection was carefully eliminated. *Drosophila melanogaster* flies normally have a slight avoidance of air scented with essence of peppermint oil. Given a choice of pure and scented air, only 35 per cent of the normal flies chose the scented air. During 21 experimental tests, 2 showed 50 per cent or more preference, 5 showed 40–49 per cent, 7 showed 30–39 per cent, and 7 showed only 22–29 per cent preference for the peppermint scented air. Freshly-hatched experimental flies that had been raised in a medium containing 0.5 per cent peppermint essence showed 67.0 per cent preference for scented air. This confirmed and extended the earlier work of Thorpe and Jones (1937) and of Thorpe (1938) on conditioning parasitic insects for new hosts. Significant as the work is, it does not prove that conditioning can prevent or even drastically reduce gene flow between the two kinds of environment if they are "available in mosaic distribution."

As stated in the previous section, the role of conditioning is that it assists in the invasion of new habitats by conspecific populations. However, extrinsic factors will have to inhibit gene flow to and from these new populations to permit them to develop into separate species.

The discussion of conditioning is not complete without reference to "locality conditioning." Thorpe (1945) is correct in giving much weight to the degree of sedentariness and the homing ability in the speciation process. As Rensch and others have pointed out (Mayr, 1942), the less the degree of dispersal in a species—and homing as well as locality conditioning cuts down dispersal—the greater the extent of speciation and incipient speciation. It is well known that in social insects, as well as in adult birds and many other animals, there is an amazing degree of *Ortstreue*. However, even though this phenomenon serves to lower the magnitude of the dispersal factor m (Wright, 1943), it by no means eliminates it completely. Dispersal operates in social insects through the nuptial flights, and in birds through the scattering of the juveniles. Least of all can such "locality conditioning" lead to the fission of a local population into several sympatric ones. The importance of *Ortstreue* is that it enhances the efficiency of external barriers. The role of this and other intrinsic factors is discussed in another publication (Mayr, 1948b).

(*d*) *Preadaptation.* Preadaptation plays an important role in several of the hypotheses associated with sympatric speciation. It is postulated that individuals actively search for the habitat for which they are preadapted. Needless to say, there is not a shred of evidence for this claim. There is a dispersal phase in the life cycle of every species during which many individuals are carried onto unsuitable locations and perish. Others may survive during favorable seasons and form the nucleus of a new population only to be wiped out again during the first adverse season. Finally, an occasional individual may have an unusually favorable gene combination which will permit some of its descendants to flourish in the new locality. This can be observed all the time along the ecological and geographical margin of the range of a species. I know of no evidence, however, that would indicate that a dispersing individual ever actively searches for a habitat for which it is "preadapted."

Difficulties Created by the Hypothesis of Sympatric Speciation

Sympatric speciation is usually postulated to explain certain ecological aspects in the speciation pattern which some authors consider inexplicable by geographic speciation. These authors overlook that sympatric speciation creates new difficulties that are avoided by the theory of geographical speciation. These difficul-

ties can essentially be classified in two groups.

(*a*) *Neglect of dispersal.* Dispersal is conspicuously neglected in all schemes of sympatric speciation, even though it is one of the basic properties of organic nature. There is a dispersal phase in the life cycle of every species. It is the adult stage in most insects with wingless larvae. In these species mating usually does not take place on the host or food plant, and hence there is no reproductive isolation between the various host races.

But, even where mating takes place on the food plant, there is a dispersal period at one stage of the life cycle. If a form, which usually lives on plant *a*, develops some individuals which colonize plant *b*, there is no reason why the offspring of the *b* individuals should not recolonize plant *a*, nor why there should not be repeated colonizations from *a* to *b*. Thus the conditions are not favorable for the establishment of a discontinuity if there is no spatial isolation between *a* and *b*. The same is true for host selection in parasites.

It is known that certain birds are extremely sedentary and live throughout the breeding season or even throughout their adult life within a restricted territory. However, even in these species, there is a certain amount of dispersal before the juvenile takes up its first territory. There seems no logical connection between the first and the second part of the statement: "Birds tend to be strongly territorial animals and the claim that geographical isolation always precedes other kinds of isolation seems premature" (Thorpe, 1945). Territoriality is a property of individuals, while speciation deals with populations.

Sessile marine organisms always seem to have a larval stage in which they may be dispersed by ocean currents for hundreds of miles and during which the populations within this area are thoroughly mixed up. This factor is often overlooked as, for example, by Test (1946) in her thesis of sympatric species in the limpets of the genus *Acmaea*. Ecological isolation, in order to be effective, must be able to prevent the mixing of the to-be-separated populations in spite of dispersal.

There are quite a number of cases among insects where the female ordinarily does not leave the host plant or where she selects the medium for egg-laying before fertilization. Among the scolicid beetles, for example, the females bore holes under the bark. The males search them out in these tunnels and mate with them there. Here appears to be a potential mechanism for the rapid development of new monophagous races. Unfortunately, none of these cases has ever been carefully analyzed. Furthermore, even in such a scheme there are many difficulties for sympatric speciation, such as the dispersal of the males and of the young females, as well as the reversibility of all conditioning that is not genetically reinforced.

(*b*) *Genetic difficulties.* The most serious weakness of most schemes of sympatric speciation is that they make untenable genetic assumptions. The principal one is that mutations produce new "types" as if genetic change was an "all or nothing" mechanism. Actually new mutants in diploid bisexual animals always occur first in heterozygous condition. Such heterozygotes will form the bridge between individuals with the new character in homozygous condition and the individuals of the parental population. To escape this difficulty all sorts of auxiliary assumptions have to be made. A new isolating mechanism cannot appear as a dominant mutation *A* because the single bearer (*Aa*) of such a mutation would at once be effectively isolated from all other individuals of his species. Furthermore, there is much evidence, to be discussed below, that a single mutation will not produce such a drastic result as complete reproductive isolation without simultaneous deleterious effects on viability.

Hence, genetic models of sympatric speciation customarily operate with recessive

mutations. C. Stern (*in litt.*) suggested to me the following mechanism [his wording slightly modified by me]:

"Let the animal *AA*, which is host specific on plant 1, have the mutation *a* which in homozygous condition produces host specificity for plant 2. Let us then make the following assumptions:

"Assumption 1: Let *AA* live only on plant 1.
"Assumption 2: Let *aa* live only on plant 2.
"Assumption 3: Let the heterozygotes *Aa* be exactly like *AA*.
"Assumption 4: Let there be little or no dispersal in the reproductive phase so that *A* animals do not meet *aa* animals.
"Assumption 5: Let *A* be ill adapted to plant 2.
"Assumption 6: Let *aa* be ill adapted to plant 1.
"Assumption 7: Let segregated *aa* formed on plant 1 have difficulties in finding plant 2, even though the original *aa* found 2.

"Then there will be little mixing between the populations on 1 and 2 and the opportunity is provided for a gradual piling up of additional genetic differences between these populations."

In this scheme seven separate assumptions are made, of which at least four are necessary to have the scheme work. The present example involved a shift in the genetic basis for habitat preference. Schemes that work with the time element are dependent on a similar pyramiding of arbitrary assumptions. One such scheme may be formulated as follows:

"Let there be a species *AA* which breeds from April 1–15, let there be in this species a mutation *a* which in homozygous condition shifts the breeding season to the period April 25–May 10 . . . etc. etc." Some of the objections to the assumptions made in this scheme are the following:

(1) It is highly unlikely that such an important part of the life cycle of the species as the breeding time ever depends on a single gene. In fact, there will be a selective premium to have in every population a number of factors in balanced condition that affect the breeding season.

(2) If a mutation occurs in one of these loci, it may shift the onset of breeding by a few days, but it is very unlikely that such a mutation would be so drastic as to eliminate overlapping of the breeding seasons.

(3) If there had been available a period suitable for breeding adjoining the present breeding period, it would have long since become incorporated into the breeding season in view of the normal fluctuation of the breeding season in a large population of individuals and the ever-present mutation pressure.

(4) The gene complex of an organism has been selected for thousands of generations to find optimum ecological conditions for the growth of its offspring in the period immediately following the breeding season. The offspring of individuals suddenly shifted out of their normal breeding season would be at a strong selective disadvantage.

A population can become adapted for a new breeding season only slowly by a gradual genetic reconstruction. Geographical isolation is necessary to permit this process to go on undisturbed. The shift of the breeding season is usually associated with a shift into a new breeding range where the changed season is advantageous.

The same arguments hold when a shift from diurnal to nocturnal breeding is involved or any of the other schemes that operate with time as the isolating factor.

The usual assumptions made both in the habitat preference and in the seasonal isolation schemes are

(1) that the heterozygotes are like one of the homozygotes,
(2) that the two phenotypes (for habitat preference or breeding season) are discontinuous, that is, that a single mutation ($A \rightarrow a$) produces complete isolation, and
(3) that—in the case of habitat selection—mating takes place in the newly-adopted habitat.

Although all three assumptions are possible, in particular 1 and 3, the relevant evidence is only rarely produced. The most vulnerable assumption is that a

harmonious, viable mutation can produce such striking effects as postulated under 2.

The whole subject is still dominated by the early De Vriesian thesis of the origin of species by single mutations. Unfortunately, no data are available on the number of gene differences between newly arisen and parental species, but some information is available on the order of magnitude involved. The weakness of such considerations is, of course, that not only the quantity but also the quality of mutations is important. A mutation on a single locus may be more important in affecting isolation between two populations than the mutations of one hundred other loci.

All individuals in sexually reproducing species (except identical twins) can be expected to be genetically different or, to put it in other words, to differ by several mutations. These are not merely minor changes, but may include a high percentage of lethals as shown by the work in *Drosophila*. There is much evidence, on the basis of morphological, physiological, immunological, and pathological studies, that two individuals of a single interbreeding human population may differ by hundreds of genes. If iso-alleles are at all common, as indicated by the work of Stern, the number of gene differences may actually be a multiple of the maximum figure now proposed.

It has not been possible in most present studies to give more than a minimum estimate of gene differences. Charles and Goodwin (1943) calculated that the morphological differences between the leaves of two hybridizing species of goldenrods (*Solidago sempervirens* and *S. rugosa*) depended on a minimum of 21 loci. The flower characters of different geographical populations of *S. sempervirens* differed by a minimum of 5–9 genes (Goodwin, 1944). Unfortunately, the method does not permit calculation of the real number of differences, which may well be 10 or more times the minimum number. Boyce (1946) showed that the often-quoted calculations are invalid which attempted to prove that a high protein strain of corn differed in at least 20–40, but possibly 200–400 genes from the original strain. Such a tremendous genetic difference between closely related strains, if confirmed, would have been most significant. Irwin and Cumley (1947) have shown that about one-half of the total number of chromosomes are involved in the serological differences between two species of doves of the genus *Streptopelia* (Senegal and Ring Dove). C. C. Tan (1946) showed that there are many genetic factors which control the isolating mechanism between *Drosophila pseudoobscura* and *D. persimilis*, and that they are mostly located in the X and the second chromosome. Sketchy as these data are, they indicate that even closely related species differ in a large number of genes.

The degree of morphological difference between two species is an exceedingly unreliable measure of the number of genic differences between them. Many sibling species of *Drosophila* are virtually indistinguishable morphologically even though they may differ by scores, if not hundreds, of genes. This is indicated by their cytological, ecological, and physiological differences, as well as by their partial or complete sterility. It is for this reason also doubtful whether Shull (1945, 1946) is correct in assuming that in two species of lady beetles of the genus *Hippodamia* "no large number of mutations would be required to evolve one species from the other or both from a common stock."

If the acquisition of reproductive isolation were a matter of a single gene mutation, one would expect isolating mechanisms to be simple. However, most isolating mechanisms between closely related species that have been studied thoroughly were found to be multiple. There always seem to be involved (a) differences in the ecological requirements, (b) reduction of the mutual sexual stimulation, and (c) reduction in the number and the viability of the offspring. On close analysis even these three categories turn out to be composite. For example, the mutual

sexual stimulation may be reduced simultaneously by differences in scent, color patterns, rhythm and pattern of display movements.

There is a selective advantage in this multiplicity for two reasons. One is that there is less loss of zygotes if a species is to rely on the mutually reenforcing action of a number of different mechanisms rather than on a single one which is subject to an occasional breakdown. The other reason is that the isolating mechanisms must protect the species from interbreeding not only with one but with *all* related species. It is very unlikely that a single mechanism will furnish complete protection against all other species. Finally, there are no genetic difficulties in gradually building up a multiple isolating mechanism in spatially segregated populations.

Before closing the discussion on the possible genetic basis of sympatric speciation, a word needs to be said about "specific modifiers." As Muller (1942) has pointed out, there will be a selective advantage for genes that act to increase the adaptiveness of the expression of one allele as compared to others, if there is a discontinuity in the factor to which the gene reacts. However, since habitat preference and mate preference are not controlled by the same gene, it becomes necessary that two sets of specific modifiers develop simultaneously. The probability that this will occur unassisted by a geographical segregation of populations is obviously very small. This is one of the reasons why the evolution of mimetic polymorphism in certain species of butterflies did not lead to the origin of a considerable number of new species, even though specific modifiers were involved.

The Hypothesis of Sympatric Speciation is Unnecessary

The principal reason why a hypothesis of sympatric speciation is usually proposed is that certain taxonomic or ecological phenomena are believed to be incompatible with geographical speciation. It shall be the aim of this section to show that these phenomena are by no means in conflict with geographical speciation. The objections that have been raised are based on misunderstandings.

The species as an aggregate of ecologically different populations. Ecological conditions vary throughout the range of all but the most narrowly distributed species. Thus every population of a species lives in a somewhat different environment and its genotype was evolved by selection for this specific local environment. What is true for local populations is even more true for subspecies. Every geographical race shows certain ecological differences from other geographical races. It was Turesson (1922) who was the first to point this out emphatically. The taxonomist who looks at these populations looks at them from his special point of view. He investigates whether such populations show morphological differences that would be of diagnostic value. If they do, he calls such populations or groups of population subspecies. The ecologist, on the other hand, looks for ecological differences between such populations (whether or not they are morphologically characterized). If he finds such differences he calls the populations ecological races or, if he is a botanist, ecotypes. In much of the current literature these two categories, the subspecies and the ecological race, are treated as two completely distinct phenomena. The truth, however, is that they are merely two facets of a single phenomenon. Gregor (1946) has recently stated correctly that if "the term 'ecotype' [is applied] to any population differentiated in respect of any characteristic attributable to the selective action of ecological factors . . . the majority of taxonomic subspecies and varieties will on experimental examination be found to bear ecotypic characteristics." I am willing to go even further than this. I am convinced that it will be a long time before even a single subspecies is found which does not bear ecotypic characteristics. Not only has every subspecies eco-

typic characteristics, but even within most subspecies are numerous ecologically different populations. Also, ecotypes do not live in an indiscriminate mixture; they are spatially segregated from each other, even though they may intergrade marginally. Ecotypes are populations or groups of populations and so are subspecies. Botanists (e.g. Gregor, 1944, 1946), on the whole, have realized this fact more clearly than have animal taxonomists.

The closest approach to geographical races in identical environment is perhaps found on some tropical islands, but even here there are stronger ecological differences than are usually recognized. The size and the elevation of the islands are different and with them temperature and precipitation. Different islands are often situated in different ocean currents, even though in close proximity. Most important of all, however, since each island has a fauna and flora which arrived fortuitously, the composition of the biota will be different on each island. In consequence, the biotic environment of a given species will be different even where the climatic environment is the same. It was Darwin (1859) who discovered this principle: "How has it happened in the several (Galapagos) islands situated within sight of each other, having the same geological nature, the same height, climate, etc., that many of the immigrants should have been differently modified, though only in a small degree. This long appeared to me a great difficulty; but it arises in chief part from the deeply-seated error of considering the physical conditions of a country as the most important for its inhabitants; whereas it cannot be disputed that the nature of the other inhabitants with which each has to compete is at least as important, and generally a far more important element of success. . . . When in former times an immigrant settled on any one or more of the islands, or when it subsequently spread from one island to another, it would undoubtedly be exposed to different conditions of life in the different islands, for it would have to compete with different sets of organisms. . . . If then it varied, natural selection would probably favour different varieties in the different islands" (Darwin, 1859).

The converse is equally true. I do not know of a single ecological race which is not at the same time at least a microgeographic race. This means that random contact between individuals belonging to the two populations is drastically reduced by distance and barriers, and the gene flow between the two populations is reduced in a parallel manner. To repeat, all geographical races are also ecological races, and all ecological races are also geographical races.

The crucial question from the point of view of sympatric speciation, however, is not whether ecological evolutionary divergence exists within a species, but whether it may lead to the origin of discontinuities without spatial segregation. I recorded as a case of non-genetic local variants a small colony of Yellow Wagtails (*Motacilla flava*) which had become accustomed to build their nests in Artemisia plants rather than on the ground (Mayr, 1942). Thorpe (1945) quotes this as an incipient sympatric isolating mechanism. The fact is that such fads, either by individuals or by local populations, are quite common in animals. But there is no evidence that they are primary isolating mechanisms. They are reversible and usually disappear as quickly as they appear. Furthermore, if they last, they lead only to the establishment of new intraspecific populations, not to new species. As shown above in the section on the invasion of new habitats, no case has yet been found where a shift in habitat preference, without geographical segregation, has given rise directly to a new species. In the cases described by Mayr (1942) and Miller (1942) of habitat differences within species of birds, geographical segregation is invariably involved. All the various Song Sparrow races with different ecological require-

ments to which Thorpe refers are geographically segregated.

The ecological specialization of geographical races may be far reaching. The ornithological literature abounds with cases of ecological difference between geographical races of a single species: one in coniferous woods, the other in deciduous; one in the lowlands, the other in the high mountains; one feeding largely on ants, the other largely on beetles, etc. One of the chief diagnostic characters of the various geographic races of the Red Crossbill (*Loxia curvirostra*) is the size and the shape of the bill. Long after these various races had been described, it was found that there was a close correlation between bill structure and the principal food in a given region. The food of the Crossbill consists of the seed of conifers. "The Crossbills inhabiting isolated spruce (*Picea*) forests have weak, small bills (for instance *Loxia curvirostra himalayensis*,[2] *L. c. altaiensis*). On the contrary, the Crossbills inhabiting isolated pine (*Pinus*) forests have big bills (for instance, *L. c. mariae* [Crimea], *L. c. polyogyna* [Tunisia], and *L. c. balearica* [Balearic Islands])" (Kirikov, 1940). The most interesting aspect of these host-adapted races of the Crossbill is that they are geographical races. In each region a geographical race evolved which is optimally adapted for feeding on the most common conifer of the region. In the few cases where spruce and pine races of the Crossbill are now found in close proximity or even interdigitating, the evidence indicates that this is a secondary development.

The most thorough analysis of adaptive features in geographical races of birds is Lack's (1947) study of Darwin's finches (Geospizinae). Most of the geographical races are shown to differ ecologically, but no evidence is found for the sympatric evolution of these ecological races. Amadon (1947) in a similar fashion has shown the importance of geographical isolation for the development of races of Drepaniidae that are strikingly different in their ecologies.

The picture that emerges from all recent studies is that species show an amazing degree of local adaptability. Species adjust themselves to every occupied environment within the boundaries of their range. As long as these populations are in contiguous contact, there is no serious reduction of gene flow. The ecological variability within a species results in increased intraspecific variability and thus furthers evolutionary divergence. Without an extrinsic reduction of gene flow, however, the ecological variability cannot become a primary source of discontinuity.

The ecological differences between species. In her review of speciation among the limpets of the genus *Acmaea* Test (1946) makes the following statement: "Along the west coast of North America occur nine species of one subgenus (*Collisella*) affording every indication of close relationship, yet having either completely concurrent or encompassed ranges. In as much as the obviously parental form has the greater range in every instance in which the range of one species is encompassed by that of another . . . it becomes practically impossible to explain the situation in terms of geographical speciation." I have quoted this statement in full because it is quite typical of the reasoning of the authors who believe in sympatric speciation. What Test found for *Acmaea* is true for the species of nearly every polytypic genus. Among birds the woodwarblers (*Dendroica*), the buntings (*Emberiza*), the white-eyes (*Zosterops*), the whistlers (*Pachycephala*), the weavers (*Ploceus*), and the hawks (*Accipiter*)—to mention only a few genera—afford good examples of closely related sympatric species. There are many even more impressive examples among insects (*Drosophila, Anopheles, Aedes*) and in other groups of invertebrates. When these groups of closely related, partially or wholly sympatric spe-

[2] Feeds mainly on larch (*Larix*) (Lack, 1944b).

cies are studied carefully, it is found—with rare exceptions—that each of the species has its own ecological niche. It is this observation which serves as the starting point for the hypothesis of sympatric speciation by ecological segregation. It is argued that since these species are partially sympatric their ecological differences could not have developed in geographical isolation. Lack (1944, 1947) has submitted a different interpretation. He shows conclusively that on the basis of the Gause (1934) principle no two related species can persist in the same locality without possessing ecological differences. Ecological difference between related sympatric species is thus merely proof for the efficacy of competition and natural selection but not for any particular method of speciation. There is no conflict whatsoever between the fact that related species differ ecologically and the assumption that they have originated by geographical speciation (Mayr, 1948b). It is fully consistent with the known facts to assume that the ecological differences had previously been developed in geographical segregation.

Reputed Instances of Sympatric Speciation

The most convincing proof for the importance of geographical speciation is the abundance of incipient cases. Hence, if there is an additional process of sympatric-ecological speciation, it should be possible to find for it also incipient cases. Indeed, there are numerous taxonomic and ecological situations that have been interpreted in the past as constituting such incipient cases. It will be shown in this section that the evidence in these cases is misinterpreted and that the facts are completely consistent with the theory of geographical speciation. The relevant phenomena can be organized under four headings: sibling species, lake swarms, secondary zones of intergradation, and insufficiently analyzed cases.

(1) *Sibling species.* Many of the cases of so-called "ecological or physiological" races of the literature are nothing but sibling or cryptic species. There is no evidence that these sibling species have evolved in any other way than by geographical speciation. This has been discussed elsewhere (Mayr, 1942, 1948a) in considerable detail and this point does not need to be taken up again.

(2) *Lake swarms.* It is well known that "species flocks" occur in all the larger and older freshwater lakes. This has been found independently by the students of fishes, crustaceans, mollusks, and other freshwater organisms. There are, for example, 178 species of Cichlid fishes in Lake Nyasa in East Africa and more than 300 species of Gammarid crustaceans in Lake Baikal. Lake Lanao on the island of Mindanao in the Philippines, the large lakes of Celebes, and other tropical and subtropical lakes in all parts of the world are also famous for their rich endemic faunas. Since it seems at first sight impossible to conceive that these sympatric faunas could have originated by geographic speciation, Woltereck, Herre, and others have postulated various processes of "explosive" speciation. None of these proposed schemes was ever worked out in detail, but they all convoke either macrogenesis (the origin of new systematic categories by a single mutation step) or various forms of homogamy (assortive mating) (e.g. Kosswig). The objections to such theories have been discussed above.

The fact that the species of these swarms are now sympatric and that they live according to the Gause principle in different ecological niches in order to minimize competition has led previous authors astray. Rensch (1933) has indicated the right solution. It is that these species have come into contact only after they had evolved and after they had acquired their ecological differences. It is sometimes thought that the 58 endemic species of Cichlids in Lake Victoria (east Africa) developed since that lake originated (i.e. during the past 20,000–50,000 years). Everything we know about the

rate of speciation (in fishes and other animals) is opposed to this conclusion. There are now 223 species of fish known from Lake Nyasa, including 194 endemic ones. Of the 178 species of Cichlidae 174 are endemic. These are divided in many genera, of which the genus *Tilapia* is comprised of six species in Lake Nyasa, four of which are endemic (Bertram, Borley, and Trewavas, 1942). Among these six species three are quite distinct, while the other three are difficult to distinguish. One of these three species is restricted to the north end of the lake (*T. karongae*), the second one (*T. squamipinnis*) occupies a zone near the shore, while the third species (*T. lidole*) appears to inhabit a more pelagic although overlapping zone. The females of the inshore species, especially those carrying fry, enter river mouths and inlets. The interesting point here is that apparently complete facilities exist for gene flow between these species if it were not prevented by sexual isolation. The ecological specialization has not reached the point where it would prevent contact between individuals of these species in breeding condition.

"Old fresh-water lakes are, for fresh-water faunas, very much what old islands are for terrestrial faunas. They permit the survival of old elements which have long since become extinct in the surrounding areas. It seems to me that students of fresh-water faunas have vastly underestimated the age of the species with which they are working. The evidence for this is quite overwhelming for Lake Baikal, Lake Tanganyika, Nyasa, and so forth. The statement by the proponents of explosive speciation that ecological speciation precedes the establishment of discontinuity is not in the least plausible, if we remember that these habitats are in continuous contact with each other and that there is no evidence for the establishment of biological isolating mechanisms as long as unrestricted interbreeding takes place between the inhabitants of the different sympatric ecological niches. On the other hand, no objections seem to exist against the assumption that species flocks originated by multiple colonizations, corresponding to the double and triple colonizations and the archipelago speciation among island animals" (Mayr, 1942).

None of the lake flocks has so far been analyzed from a broader point of view. Such questions need to be answered as: What species are found only in part of the lake, like *Tilapia karongae* in northern Lake Nyasa? What species have discontinuous ranges within a given lake? Are the nearest relatives of a given species found in the same lake, or in some neighboring tributary or other lake? Has the inventory of the freshwater faunas of all the present and former tributaries of these lakes been completed and how do these faunas compare with the lake fauna?

A recent analysis of the faunas of the lakes of central Asia has had the unexpected result to show that many of the famous "endemics" of Lake Baikal have, in fact, a rather wide distribution. Lake Baikal is indeed a living museum preserving the remnants of several freshwater faunas that were formerly widespread in central Asia (Kozhov, 1946). The exact geological age of a given lake is rather irrelevant if it has become the receptacle of previously existing faunas. Lake Lanao in Mindanao may have originated within the late Pleistocene, but it contains an apparently Tertiary fauna which may have originated in several separate river systems. Trewavas (1947) suggests that the sudden rise or fall of water level in a lake may be a factor in speciation. This is improbable if the entire lake shore is inhabited by a continuous population living everywhere under identical conditions. Her scheme, however, works very well if, for example, a number of disconnected estuaries are involved, each with somewhat different conditions. A sudden rise of water level may wipe out all but the few most pelagic individuals in a shallow estuary, while in a deep estuary the entire population may move simply inland with the shore line. If the isolation has lasted

sufficiently long, the more pelagic population can move into the estuary of the inshore species without hybridizing. The result would be two ecologically different and partially sympatric species.

There must be situations where one might be able to study the origin of a species flock *in statu nascendi*. Hubbs and Raney (1946) have recently described such a potential case. In Lake Waccamac in North Carolina each of the genera *Notropis, Fundulus, Boleosoma,* and *Menidia* has developed an endemic form during the last quarter of the Pleistocene. These streamlined lake forms may or may not be reproductively isolated from their allopatric ancestral forms. However, if repeated invasions of the respective species complexes would occur, after reproductive isolation had been established, it would lead to the formation of species flocks. The environment in the lake is very different from the environment of the tributary streams and this undoubtedly leads to a considerable acceleration of the evolutionary rate. In this respect lakes are very much like islands, as pointed out before (Mayr, 1942). However, even though the rate of evolutionary divergence is much accelerated, there is no evidence that the origin of discontinuities differs in principle from that in terrestrial animals.

(3) *Secondary contiguity of ecologically different subspecies.* An ever increasing number of cases is being described in the literature where two ecologically very distinct subspecies are found to have adjacent or even interdigitating ranges. Such cases are often quoted as proving sympatric speciation. Actually, there is, of course, in these cases nearly always spatial segregation and, furthermore, it can often be demonstrated that the present contiguity is a rather recent phenomenon. In the mayfly *Stenonema interpunctatum* there are four intergrading subspecies with only partially separated ranges (Spieth, 1947). Most of the range of *S. i. heterotarsale* in the Lake Erie-Ontario region is overlapped by the subspecies *canadense* and *interpunctatum*. "Obviously there must be a definite survival value attached to each of the populations or they would quickly fuse into one variable one." *S. i. interpunctatum* and *canadense* emerge earlier in the season, *heterotarsale* later. On the basis of the present distribution pattern it appears probable that the four subspecies originated during the Pleistocene in the following districts: *interpunctatum* in the Mississippi valley, *canadense* in Canada, *frontale* on the U. S. Atlantic coast, and *heterotarsale* in the Lake Erie-Ontario district. Most of the present range overlaps are due to the post-Pleistocene range expansions of *interpunctatum* and *frontale*. The most interesting aspect of this case is that during their geographical segregation each of these forms acquired a number of physiological characteristics or adaptations to special, narrow ecological niches so that now several of these "subspecies" can live in various parts of the same stream without losing their identity.

Similar cases have been described in fishes. The nominate race *nigrum* of the small fish *Boleosoma nigrum* has a very wide range in the United States. Within its range is found the subspecies *eulepis* which is more completely scaled on cheeks, nape, and breast. The nominate race occurs in lakes and streams with a firm (sandy or rocky) substratum, while *eulepis* is a fish of estuaries, rather extensive and quiet or slow-moving lowland waters, characterized by moderate or dense growths of aquatic vegetation, and on bottoms composed at least in part of mud or silt. The interesting aspect of this case is that the range of *eulepis* consists of more or less discontinuous pockets or foci of abundance, surrounded by peripheral areas of intergradation with the nominate race, but more or less restricted to the Great Lakes region. The morphological differences are not phenotypic modifications through life in the specific habitat niche, but have a genetic basis as shown by Lagler and Bailey

(1947). Physiological differences (oxygen and temperature tolerance, etc.) are presumably associated with the morphological ones, but they have not yet been investigated. There are two alternative explanations of this case. Either one presumes that in each stream and lake a quiet-water race developed in spatial segregation, or one believes that the present proximity of the races is a secondary phenomenon. Although both solutions are possible, I tend to the second one for two reasons. In many "*eulepis* habitats" in the range of *nigrum*, this subspecies appears to be absent, particularly in that part of the range of *nigrum* that is outside the Great Lakes region. The second reason is the comparative homogeneity of *eulepis* in its now disjunct range. The available evidence suggests that *eulepis* once had a continuous range (? during one of the later stages of the Pleistocene) but that the somewhat superior *nigrum* invaded its range and forced it to retreat into the quiet water pockets where *eulepis* is superior. It would be very interesting to know more about the genetic mechanisms that prevent the breaking up of the *nigrum*- and *eulepis*-gene complexes that are superior in their respective habitats. That such mechanisms seem to exist is indicated by the work of Heuts (1947) on the races of the Stickleback (*Gasterosteus aculeatus*) in western Europe. In this case again two rather distinct races or race-complexes seem to have come into secondary contact without losing their identity.

In polymorphic populations there is also sometimes evidence that each of the various types has originated in a definite locality. Much of the evidence concerning mimetic polymorphism in butterflies points that way and Southern (*in litt.*) suggests that such spatial segregation may have been involved in the development of host races in cuckoos. During periods of range expansions, it can sometimes even be demonstrated that some "ecologically variable" species consist actually of various ecotypes, each of which has a different geographical origin (Peitzmeier, 1942).

This evidence can be summarized in the statement that it appears that ecologically contrasting subspecies normally originate in spatial segregation and usually even in complete geographical isolation. Contact zones between such subspecies are usually zones of secondary intergradation (Mâyr, 1942).

(4) *Insufficient evidence.* Sympatric speciation is often postulated in cases in which the available evidence is insufficient to draw any conclusions. Vaghin (1946), for example, uses it to account for the presence of two forms of the oligochaet *Chaetogaster limnaei* in mollusks, one a commensal in the mantle, the other an endoparasite in the kidney. No evidence is given on the question whether or not the two populations are reproductively isolated. They might be two good (sibling) species which have invaded the host at different times, but they might also be members of a single population which acquire different characteristics depending on the organ of the mollusk which they invade. This case is merely quoted as a single example of numerous similar ones that one finds continuously in the literature. They are without value for the problem of sympatric speciation unless the analysis is carried a good deal further.

The Factors of Speciation

A balanced evaluation of the respective roles in speciation of ecological and geographical factors is still missing. Both work closely together and "there is no geographic speciation that is not at the same time ecological and genetic speciation" (Mayr, 1942). The first step in the speciation process is the founding of a new intraspecific population. This is very often possible only through a shift in ecological tolerance, and insofar Thorpe's statement is quite correct that an ecological rather than a geographical event may be the first step in speciation, or—since the new population will be not only ecologically different but also spatially

segregated from the parental one—that the ecological event (adaptation to a new ecological niche) is at least simultaneous with the first geographical event. This first step leads to the establishment of a spatially segregated population that is exposed to different selection pressure owing to the more or less differing ecological conditions under which it lives. The ecological factors here lead to evolutionary divergence. These populations will drift apart genetically (probably at an accelerating rate!) until a discontinuity through reproductive isolation develops, provided extrinsic barriers reduce dispersal (= gene flow) to such an extent that it can no longer neutralize the effects of the different selection pressures in the two populations. It is still unknown whether this can happen between contiguous populations without the help of extrinsic factors that reduce gene flow.

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Summary

All degrees of geographical isolation are known, resulting in a complete interruption or only slight reduction of gene flow between the isolated populations. The term microgeographical isolation may be used where only short distances are involved.

The establishment of a new intraspecific population is usually associated with a shift in the ecological characteristics of such a population. All subspecies show ecological differences, and no "ecological races" are known that are not also at least "microgeographical."

It is unproven and unlikely that reproductive isolation can develop between contiguous populations.

Many of the assumptions made in the various hypotheses of sympatric speciation are erroneous. The evidence usually cited as proving sympatric speciation is fully consistent with the theory of geographic speciation. The concept of sympatric speciation creates many difficulties avoided by the concept of geographic speciation.

Sympatric speciation, if it occurs at all, must be an exceptional process. The normal process of speciation in obligatorily sexual and cross fertilizing organisms is that of geographical speciation.

Literature Cited

Alpatov, B. W. 1925. Über die homogame und pangame Paarung im Tierreiche. Zool. Anz., **62**: 329–331.

Amadon, D. 1947. Ecology and the evolution of some Hawaiian birds. Evolution **1**: 63–68.

Armstrong, T. 1946. Differences in the life history of the codling moth, *Carpocapsa pomonella* (L.), attacking pear and apple. Canadian Entomologist, **77**: 231–233.

Baldwin, J. M. 1902. Development and evolution. Macmillan and Company, 395 pp.

Bertram, C. K. R., J. J. H. Borley, and E. Trewavas. 1942. Report on the fish and fisheries of Lake Nyasa. Crown Agents of the Colonies, 181 pp.

Blair, W. F. 1947. Estimated frequencies of the buff and gray genes (G, g) in adjacent populations of deermice (*Peromyscus maniculatus blandus*) living on soils of different colors. Contr. Lab. Vert. Biol., **36**: 1–16.

Boyce, A. M. 1935. The codling moth in Persian Walnuts. Jour. Econ. Ent., **28**: 864–873.

Boyce, S. W. 1946. Estimation of genes in inheritance of quantitative characters. Nature, **157**: 657.

Catchpool, E. 1884. An unnoticed factor in evolution. Nature, **31**: 4.

Charles, D. R., and R. H. Goodwin. 1943. An estimate of the minimum number of genes differentiating two species of goldenrod with respect to their morphological characters. Amer. Nat., **77**: 53–69.

Crozier, W. 1918. Assortative mating in a nudibranch, *Chromodoris zebra*. Jour. Exp. Zoöl., **27**: 247–292.

Cushing, J. E. 1941. An experiment on olfactory conditioning in *Drosophila guttifera*. Proc. Nat. Acad. Sci., **27**: 496–499.

Dahl, E. 1889. Die Bedeutung der geschlechtlichen Zuchtwahl bei der Trennung der Arten. Zool. Anz., **12**: 262–266.

Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life. John Murray, London.

DIEDERICH, G. W. 1941. Non-random mating between yellow-white and wild types of *Drosophila melanogaster*. Genetics, **26**: 148.

DOBZHANSKY, TH., AND E. MAYR. 1945. Experiments on sexual isolation in *Drosophila*. IV. Modification of the degree of isolation between *Drosophila pseudoobscura* and *Drosophila persimilis* and of sexual preferences in *Drosophila prosaltans*. Proc. Nat. Acad. Sci., **31**: 75–82.

GAUSE, G. F. 1934. Struggle for existence. Williams and Wilkins Company, 160 pp.

——. 1947. Problems of evolution. Trans. Conn. Acad. Arts and Sciences, **37**: 17–68.

GERSHENSON, S. 1941. Additional data concerning the mating system in wild populations of common hamster (*Cricetus cricetus*). Compt. Rend. Acad. Sci. URSS, **31**: 155–156.

GOODWIN, R. H. 1944. The inheritance of flowering time in a short-day species, *Solidago sempervirens* L. Genetics, **29**: 503–519.

GREGOR, J. W. 1944. The ecotype. Biol. Reviews, **19**: 20–30.

——. 1946. Ecotypic differentiation. New Phytologist, **45**: 254–270.

HEUTS, M. J. 1947. Experimental studies on adaptive evolution in *Gasterosteus aculeatus* L. Evolution **1**: 89–102.

HOGBEN, L. 1946. An introduction to mathematical genetics. W. W. Norton and Co., Inc., 260 pp.

HUBBS, C. L., AND E. C. RANEY. 1946. Endemic fish fauna of Lake Waccamac, North Carolina. Misc. Publ. Mus. Zool., Univ. Mich., No. 54, 30 pp.

IRWIN, M. R., AND R. W. CUMLEY. 1947. A second analysis of antigenic differences between species in Columbidae. Genetics, **32**: 178–184.

KIRIKOV, S. V. 1940. On the connection between the Red Crossbills and the coniferous trees. Bull. Acad. Sci. URSS (Biol.), 359–376.

KOSSWIG, C. 1947. Selective mating as a factor for speciation in Cichlid fish of East African lakes. Nature, **159**: 604.

KOZHOV, M. 1946. Baikalian mollusks from Lake Kossogol (Mongolia). Compt. Rend. (Doklady) Acad. Sci. URSS, **52**: 365–368.

LACK, D. 1944a. Ecological aspects of species formation in passerine birds. Ibis, **86**: 260–286.

——. 1944b. Correlation between beak and food in the Crossbill, *Loxia curvirostra* Linnaeus. Ibis, **86**: 552–553.

——. 1947. Darwin's finches. Cambridge University Press, 208 pp.

——. 1948. The significance of ecological isolation. [Princeton Symposium.] [In press.]

LAGLER, K. F., AND R. M. BAILEY. 1947. The genetic fixity of differential characters in subspecies of the percid fish, *Boleosoma nigrum*. Copeia, 50–59.

MANNING, T. H. 1942. Blue and lesser snow geese on Southampton and Baffin Islands. Auk, **59**: 158–175.

MASING, R. A. 1946. Experiments on selection for selective egg-deposition in *Drosophila melanogaster*. Comptes Rend. Acad. Sci. URSS, **51**: 393–396.

MAYR, E. 1942. Systematics and the origin of species. Columbia University Press, 334 pp.

——. 1948a. The bearing of the new systematics on genetical problems. Advances in Genetics, 2 (in press).

——. 1948b. Speciation and systematics. Princeton Symposium (in press).

MEYER, N. F., AND Z. A. MEYER. 1946. The formation of biological forms in *Chrysopa vulgaris* Schr. (Neuroptera, Chrysopidae). Zool. Jour., **25**: 115–120.

MILLER, A. H. 1942. Habitat selection among higher vertebrates and its relation to intraspecific variation. Amer. Nat., **76**: 25–35.

MULLER, H. J. 1942. Isolating mechanisms, evolution and temperature. Biological Symposia, **6**: 71–125.

PEARSON, K. 1900. The grammar of science. Second ed., Adam and Charles Black, London, 548 pp.

PEITZMEIER, J. 1942. Die Bedeutung der oekologischen Beharrungtendenz für faunistische Untersuchungen. Jour. f. Ornith., **90**: 311–322.

RENSCH, B. 1933. Zoologische Systematik und Artbildungsproblem. Verh. Deutsch Zool. Ges., 19–83.

ROMANES, G. J. 1897. Darwin and after Darwin. Vol. III, Open Court Publishing Co., 181 pp.

SHULL, A. F. 1945. Inheritance in lady beetles. III. Crosses between variants of *Hippodamia quinquesignata* and between this species and *H. convergens*. Jour. Hered., **36**: 149–160.

——. 1946. The form of the chitinous male genitalia in crosses of the species *Hippodamia quinquesignata* and *H. convergens*. Genetics, **31**: 291–303.

SPETT, G. 1929. Zur Frage der Homogamie und Pangamie bei Tieren, Untersuchungen an einigen Coleopteren. Biol. Centralbl., **49**: 385–392.

——. 1931. Gibt es eine partielle sexuelle Isolation unter den Mutationen und der Grundform von *Drosophila melanogaster* Meig.? Zeitschr. ind. Abst. Vererb., **60**: 63–83.

SPIETH, H. T. 1947. Taxonomic studies on the Ephemeroptera. IV. The genus Stenonema. Ann. Ent. Soc. Amer., **40**: 87–122.

STRESEMANN, E. 1942. Oekologische Sippen-, Rassen-, und Artunterschiede bei Vögeln. Jour. für Ornith., **91**: 305–328.

TAN, C. C. 1946. Genetics of sexual isolation between *Drosophila pseudoobscura* and *D. persimilis*. Genetics, **31**: 558–573.

TEST, A. R. 1946. Speciation in limpets of the genus *Acmaea*. Contr. Lab. Vert. Biol., **31**: 1–24.

THORPE, W. H. 1938. Further experiments on olfactory conditioning in a parasitic insect. The nature of the conditioning process. Proc. Royal Soc., **126**: 370–397.

——. 1939. Further studies on pre-imaginal olfactory conditioning in insects. Proc. Royal Soc., **127**: 424–433.

——. 1945. The evolutionary significance of habitat selection. Jour. Animal Ecol., **14**: 67–70.

—— AND F. G. W. JONES. 1937. Olfactory conditioning in a parasitic insect and its relation to the problem of host selection. Proc. Royal Soc., **124**: 56–81.

TIMOFEEFF-RESSOVSKY, N. W. 1943. [Erbliche und oekologische Isolation.] Jour. für Ornith., **91**: 326–327.

TREWAVAS, E. 1947. Speciation in Cichlid fishes of East African lakes. Nature, **160**: 96–97.

TURESSON, G. 1922. The species and the variety as ecological units. Hereditas, **3**: 100–113, 210–350.

VAGHIN, V. L. 1946. On the biological species of *Chaetogaster limnaei* K. Baer. Compt. Rend. Acad. Sci. URSS, **51**: 481–484.

VALENTINE, J. M. 1943. Insect taxonomy and principles of speciation. Jour. Washington Acad. Sci., **33**: 353–358.

——. 1945. Speciation and raciation in Pseudoanophthalmus (Cave beetles). Trans. Conn. Acad. Arts and Sci., **36**: 631–659.

WAGNER, M. 1889. Die Entstehung der Arten durch räumliche Sonderung. Benno Schwalbe, Basel.

WRIGHT, S. 1943. Isolation by distance. Genetics, **28**: 114–138.

BOOKS ON EVOLUTION RECEIVED

BABCOCK, ERNEST BROWN. 1947. The genus *Crepis*. Part I. The taxonomy, phylogeny, distribution, and evolution of *Crepis*. Univ. Calif. Publ. in Bot., vol. 21, 197 pp. Part II. Systematic treatment, vol. 22, pp. 199–1030.

HEBERER, GERHARD. 1943. Die Evolution der Organismen. Jena, Gustav Fischer, 774 pp.

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HUTCHINSON, J. B., R. A. SILOW, AND S. G. STEPHENS. 1947. The evolution of *Gossypium* and the differentiation of the cultivated cottons. Oxford University Press, 160 pp.

LACK, DAVID. 1947. Darwin's finches. Cambridge University Press, 208 pp.

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Illustrations, including maps, should be referred to as "figures" wherever possible. Plates are reserved for illustrations that require paper inserts or for collections of small figures. All figures and plates are reduced to a maximum of 4⅞ inches in width and 6½ inches in length.

All references to literature should be collected into a list of "Literature Cited" at the end of the article. See recent numbers of EVOLUTION for accepted style.

Titles should be short, preferably less than seven words. Footnote material should be incorporated in the text whenever possible.

Every article of more than a few pages should have a well-written interesting summary limited to four per cent of the length of the paper; it is to be complete in itself, and understandable without reference to the body of the article. The scope of the paper should be stated in an introductory paragraph.

Authors are requested to prepare abstracts of their papers to be returned with the proof to the Editor to be forwarded to Biological Abstracts.

Manuscripts should be addressed to

DR. E. MAYR
American Museum of Natural History
New York 24, New York.

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